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Hydnoporia, an older name for *Pseudochaete* and *Hymenochaetopsis*, and typification of the genus *Hymenochaete* (*Hymenochaetales*, *Basidiomycota*)

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Abstract: The genus name *Hydnoporia* is reinstated to encompass the *Hymenochaete tabacina* group currently addressed to *Pseudochaete* (illegitimate genus) or *Hymenochaetopsis*. Identity of the type species of *Hydnoporia*, *Sistotrema fuscescens* (= *Hydnoporia olivacea* in current sense), is clarified, and a lectotype is selected. In total, 12 species are combined in *Hydnoporia*: *H. corrugata*, *H. gigasetosa*, *H. lamellata*, *H. laricicola*, *H. latesetosa*, *H. lenta*, *H. rhododendri*, *H. rimosa*, *H. subrigidula*, *H. tabacina*, *H. tabacinoides*, and *H. yasudai*. *Hydnoporia diffissa* is described as new. Analyses of all available ITS (94) and newly produced *tef1* sequences (20) indicate that there are at least 20–27 species in the genus. Identity of the type species of *Hymenochaete*, *H. rubiginosa*, is clarified; the name is retained for the species so named in Europe while other species are present in North America and East Asia. Additionally, three new combinations in *Hymenochaete* are proposed: *H. campylopora* (= *Cyclomyces fuscus*), *H. microcycla* (= *Cyclomyces tabacinus*), and *H. saepiaria*.

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INTRODUCTION

The genus *Hymenochaete* has traditionally included all brown-coloured corticioid fungi with simple-septate hyphae and setae, which are specialized sterile cells in the basidiocarp. After the study of Patouillard (1900) the concept of the genus remained stable until the application of DNA-based phylogenetics. Affinity of *Hymenochaete* to polypores with similar micromorphology and pigmentation also became well accepted, and both species of poroid and smooth hymenophores were included in the family *Hymenochaetaceae* early on (after Donk 1933).

The genus has received considerable attention from taxonomists, and Léger (1998) recognized no less than 132 species in the only published monograph of the genus. Yet before the DNA era, few questioned the unity of *Hymenochaete*, so similar are the species morphologically. For instance, in his extensive morphological analysis Parmasto (1995) did not find grounds for splitting *Hymenochaete*.

Wagner & Fischer (2002) were the first to use genetic data to show that *Hymenochaete* in the traditional sense was polyphyletic. They divided *Hymenochaetaceae* with smooth hymenophores to two separate lineages. The name *Hymenochaete* went with the larger clade, while they described a new genus for the other lineage, *Pseudochaete*. In their analysis *Pseudochaete* contained only one, albeit common species, *Hymenochaete tabacina*.

Since then more comprehensive order-level analysis have confirmed that the corticioid species within *Hymenochaetaceae* are divided in two clades, equal to well-established polypore genera such as *Fomitiporia* and *Phellinus* (Binder *et al.* 2005, Larsson *et al.* 2006). Recent studies have provided additional molecular data on *Hymenochaete* and demonstrated that 12

additional species belong to *Pseudochaete* (He & Dai 2012, He & Li 2013, Parmasto *et al.* 2014). Even though relationships between genera of the *Hymenochaetaceae* are to some degree unresolved, these studies have shown beyond doubt that *Hymenochaete* and *Pseudochaete* are separate clades that deserve generic status.

Unfortunately, the fungal genus name *Pseudochaete* T. Wagner & M. Fisch. turned out to be a homonym of *Pseudochaete* W. West & G.S. West 1903, a genus of green algae belonging to the family *Chaetophoraceae*. Consequently, Yang *et al.* (2016) suggested a new name (*nomen novum*) for the *Pseudochaete* group, *Hymenochaetopsis* S.H. He & Jiao Yang, making the appropriate combinations.

When describing a genus for *Hymenochaete tabacina* and its relatives, Wagner & Fischer (2002) and Yang *et al.* (2016) neglected the genus name *Hydnoporia* Murrill, which is typified by *Sistotrema fuscescens* Schwein., now considered a synonym of the common North American species *Hydnochaete olivacea* (Ryvarden 1982a). Parmasto *et al.* (2014), corroborated by Yang *et al.* (2016), showed that *H. olivacea* is a close, congeneric relative of *H. tabacina*. This makes *Hydnoporia*, fungal *Pseudochaete* and *Hymenochaetopsis* taxonomic synonyms.

As a genus described in 1907, *Hydnoporia* has priority over *Hymenochaetopsis* and *Pseudochaete*. We see no good reasons for conserving *Pseudochaete* for the fungal genus and even less so for *Hymenochaetopsis*. Conservation is recommended when a name change would affect names in wide and persistent use, e.g. species of great economic value or well-known and much studied parasites. *Pseudochaete* has been in use within kingdom Fungi for 17 yr only, and *Hymenochaetopsis* just for 3 yr. Neither does the genus contain enigmatic species, and thus arguments for conservation are weak. We therefore adopt the

name *Hydnoporia* for the whole *Hymenochaete tabacina* clade, replacing *Pseudochaete* and *Hymenochaetopsis*.

In total, 14 species names are accepted in *Hydnoporia* after our revision, although true species number appears to be at least 20–27 judging from sequence data. The species range from resupinate species with smooth hymenophore to pileate and hydroid (Fig. 1). Here we have studied the *H. corrugata* and

H. tabacina species complexes more closely, resulting in the description of a new species, *H. diffissa*, and re-introduction of *H. rimosa*, an East Asian *H. corrugata* relative. *Hymenochaete intricata* is placed among the synonyms of *Hydnoporia tabacina*. In addition, the generic type of *Hymenochaete*, *H. rubiginosa*, is typified, and three other, closely related species are recognized in the *H. rubiginosa* group, although left unnamed.



Fig. 1. Basidiocarp diversity of *Hydnoporia*. **A.** *H. rimosa* (RU-KHA, Spirin 10797). **B.** *H. olivacea* (US-MA, Miettinen 15.10.2011). **C.** *H. tabacina* (US-NC, Miettinen 19630). **D.** *H. laricicola* (RU-KHA, Spirin 3810). **E.** *H. yasudai* (RU-KHA, Spirin 10812).

MATERIALS AND METHODS

We studied type specimens and collections from herbaria H, O, UPS, NY, TNS, TAAM, BPI, and GB. Herbarium acronyms are given according to Thiers (2018). Studied collections with ITS sequences are marked with asterisk (*) throughout this paper. References to the International Code of Nomenclature for algae, fungi, and plants (ICN) all follow the Shenzhen code (Turland *et al.* 2018).

We measured all microscopic structures with Leica microscopes using Cotton Blue in lactic acid (CB, Merck 1275), with $\times 1250$ magnification and phase contrast illumination. Additionally, we used 5 % KOH for microscopy to study tight hyphal structures. At least 30 basidiospores were measured per each specimen reported in Table 1. For presenting variation of hyphal width and basidiospores, the 20 % and 5 % extremes are given in parentheses, respectively (hyphal width variation is larger than spore size variation). Setal measurements are

Table 1. Basidiospore measurements of the *Hydnoporia* specimens.

Species / specimen	L'	L	W'	W	Q'	Q	n
<i>H. corrugata</i>	(4.0)4.1–5.5(6.2)	4.76	(1.5)1.6–1.8(1.9)	1.70	(2.2)2.3–3.3(3.4)	2.81	90
Michelitsch 20 Mar. 1977	(4.0)4.1–5.3(6.2)	4.86	(1.5)1.6–1.8(1.9)	1.70	(2.5)2.6–3.3(3.4)	2.87	30
Poelt 15 Sep. 1974	(4.0)4.1–5.1(5.2)	4.46	(1.5)1.6–1.8(1.9)	1.69	(2.2)2.3–3.0(3.1)	2.65	30
Volobuev 1 Aug. 2013	(4.3)4.4–5.5(5.8)	4.97	(1.5)1.6–1.8(1.9)	1.72	(2.3)2.4–3.2(3.4)	2.90	30
<i>H. diffissa</i>	(4.1)4.2–7.3(7.8)	5.28	1.7–2.2	1.92	(2.1)2.2–3.5(3.7)	2.74	90
Miettinen 17127.4	(4.7)5.1–7.3(7.8)	5.99	1.8–2.2	1.99	(2.4)2.5–3.5(3.7)	3.00	30
Miettinen 19463	(4.6)4.7–5.6(6.2)	5.18	1.8–2.1(2.2)	1.91	(2.4)2.5–3.1	2.72	30
Ryvarden 46500	(4.1)4.2–5.2(5.6)	4.67	1.7–2.0(2.1)	1.87	(2.1)2.2–2.8(3.0)	2.50	30
<i>H. laricicola</i>	(4.2)4.3–6.8(7.0)	5.27	(1.6)1.7–2.1(2.2)	1.91	(2.2)2.3–3.5(3.6)	2.78	60
Spirin 5400	(4.2)4.3–5.6(5.8)	4.91	(1.6)1.7–2.1(2.2)	1.93	(2.2)2.3–2.8(2.9)	2.56	30
Ahti 50083	(4.3)4.5–6.8(7.0)	5.63	(1.6)1.7–2.0(2.1)	1.89	(2.2)2.3–3.5(3.6)	2.99	30
<i>H. rhododendri</i>	(3.8)3.9–5.2(5.6)	4.56	(1.1)1.2–1.6(1.7)	1.33	(2.7)2.8–4.3(4.7)	3.44	90
Spirin 6450	(3.8)3.9–5.2(5.6)	4.51	(1.1)1.2–1.5(1.6)	1.29	(2.7)3.1–4.1(4.3)	3.51	30
Spirin 6476	(3.9)4.1–5.1(5.2)	4.51	(1.1)1.2–1.5(1.6)	1.29	(2.9)3.1–4.3(4.7)	3.51	30
TAAM 189353	(3.8)4.0–5.2(5.3)	4.65	(1.1)1.2–1.6(1.7)	1.42	(2.7)2.8–4.0(4.1)	3.31	30
<i>H. rimosa</i>	(4.1)4.2–6.3(6.9)	5.22	(1.7)1.8–2.3(2.5)	1.99	(2.0)2.1–3.2(3.4)	2.64	180
Spirin 5060	(4.2)4.3–5.7(6.0)	4.94	(1.7)1.8–2.0(2.1)	1.84	(2.3)2.4–3.0(3.2)	2.69	30
Spirin 5277	(5.0)5.1–5.8(6.1)	5.32	(1.9)2.0–2.3(2.4)	2.12	(2.2)2.3–2.8(2.9)	2.52	30
Spirin 5617	(4.1)4.2–5.9(6.1)	4.89	(1.8)1.9–2.3(2.4)	1.99	(2.0)2.1–2.9(3.0)	2.47	30
Spirin 5629	(4.7)5.1–6.3(6.9)	5.66	(1.8)1.9–2.2(2.5)	2.04	(2.3)2.4–3.2(3.3)	2.78	30
Spirin 5678	(4.1)4.2–5.3(5.5)	4.82	(1.7)1.8–2.0(2.1)	1.88	(2.2)2.3–2.9(3.0)	2.58	30
Spirin 6104	(4.6)5.0–6.3(6.8)	5.68	(1.8)1.9–2.2(2.4)	2.04	(2.4)2.5–3.2(3.4)	2.78	30
<i>H. tabacina</i>	(3.9)4.1–6.2(6.4)	4.93	(1.4)1.5–2.1(2.2)	1.81	(2.0)2.1–3.6(3.8)	2.74	420
Kotiranta 20693	(4.0)4.1–5.2(5.8)	4.54	(1.7)1.8–2.1(2.2)	1.89	(2.0)2.1–2.8(2.9)	2.40	30
Kotiranta 21006	(4.3)4.5–6.1(6.3)	5.20	(1.7)1.8–2.0(2.1)	1.89	(2.2)2.3–2.9(3.3)	2.75	30
Kotiranta 25205	(4.1)4.2–6.0(6.1)	4.94	1.7–2.0	1.83	(2.2)2.3–3.1(3.4)	2.70	30
Miettinen 17028.3	(4.2)4.3–5.3(6.4)	4.91	(1.5)1.6–1.9(2.0)	1.72	(2.4)2.5–3.3(3.6)	2.87	30
Miettinen 18168	(4.3)4.6–5.9(6.1)	5.16	(1.7)1.8–2.0(2.1)	1.93	(2.3)2.4–3.2(3.3)	2.68	30
Niemelä 2604	(4.1)4.2–5.8(6.4)	4.96	(1.5)1.6–1.8(1.9)	1.68	(2.3)2.4–3.5(3.6)	2.96	30
Niemelä 3581	(4.4)4.6–6.2(6.3)	5.41	(1.6)1.7–2.0(2.1)	1.82	(2.4)2.6–3.3(3.4)	2.99	30
Niemelä 8341	(5.0)5.1–6.1(6.2)	5.45	(1.7)1.8–2.0(2.1)	1.88	(2.5)2.6–3.3(3.4)	2.91	30
Ryvarden 14421	(4.1)4.2–5.7(6.0)	4.74	(1.5)1.6–1.8(1.9)	1.69	(2.2)2.3–3.4(3.6)	2.82	30
Spirin 5196	(4.7)4.8–5.9(6.0)	5.20	1.8–2.1(2.2)	1.95	(2.2)2.4–2.9(3.0)	2.67	30
Spirin 5496	(3.9)4.0–5.2(6.2)	4.37	(1.4)1.5–1.8(1.9)	1.70	(2.1)2.2–3.4(3.6)	2.59	30
Spirin 6507	(4.0)4.1–5.1(5.3)	4.51	(1.6)1.7–2.0(2.1)	1.88	(2.1)2.2–2.7(2.8)	2.41	30
Spirin 6517	(4.2)4.3–5.6(5.7)	4.76	(1.5)1.6–2.0	1.79	(2.2)2.3–3.2(3.3)	2.67	30
Spirin 6520	(4.1)4.2–6.0(6.2)	4.80	(1.4)1.5–1.8	1.64	2.5–3.6(3.8)	2.94	30
<i>H. yasudai</i>	(4.3)4.4–6.1(6.4)	5.28	(1.9)2.0–2.3(2.4)	2.09	(1.9)2.2–2.9(3.0)	2.53	30
Spirin 6475	(4.3)4.4–6.1(6.4)	5.28	(1.9)2.0–2.3(2.4)	2.09	(1.9)2.2–2.9(3.0)	2.53	30

Table 2. Setal measurements of selected *Hydnoporia* specimens.

Species / specimen	L'	L	W'	W	Q'	Q	n
<i>H. corrugata</i>	(49.8)52.1–86.0(110.9)	66.8	(6.9)7.2–14.1(17.8)	9.8	(4.5)4.7–9.6(9.7)	7.00	40
Poelt 15 Sep. 1974	(49.8)52.3–86.0(110.9)	66.9	(6.9)7.2–14.1(17.8)	10.1	(4.8)5.1–8.3(8.6)	6.77	20
Volobuev 1 Aug. 2013	(51.8)52.1–84.2(94.2)	66.6	(7.2)7.3–11.3(13.7)	9.5	(4.5)4.7–9.6(9.7)	7.23	20
<i>H. diffissa</i>	(46.8)50.7–73.0(90.2)	60.6	(6.2)6.8–11.4(12.9)	9.1	(4.7)5.0–8.8(9.2)	6.82	60
Miettinen 17127.4	(46.8)50.7–70.2(72.0)	58.2	(6.2)7.0–9.9(11.6)	8.4	(5.1)5.2–8.8(9.2)	7.08	20
Miettinen 19463	(49.8)52.7–70.3(79.8)	60.2	(6.4)6.8–11.1(11.5)	8.8	(4.7)5.0–8.1(8.6)	6.94	20
Ryvarden 46500	(50.2)53.2–73.0(90.2)	63.4	(7.9)8.0–11.4(12.9)	10.0	(4.7)5.0–7.9(8.7)	6.44	20
<i>H. laricicola</i>	(30.8)31.2–68.8(83.6)	43.9	(5.3)5.6–12.0(12.1)	8.1	(3.8)3.9–8.2(8.9)	5.41	40
Spirin 5400	(30.8)31.2–54.9(59.2)	41.0	(5.5)6.0–11.1(12.2)	8.1	(3.8)3.9–6.4(7.5)	5.16	20
Ahti 50083	(31.8)32.3–68.8(83.6)	46.8	(5.3)5.6–12.0(12.1)	8.1	(3.8)4.1–8.2(8.9)	5.86	20
<i>H. rhododendri</i>	(53.2)56.1–95.3(98.6)	71.2	(6.2)6.3–17.2(18.7)	10.5	(4.2)4.7–11.5(13.3)	7.19	60
Spirin 6450	(53.2)56.3–82.3(88.2)	68.7	(6.2)6.3–12.0(12.5)	8.7	(4.6)5.8–11.5(13.3)	8.24	20
Spirin 6476	(54.3)56.1–95.3(98.6)	74.0	(8.2)9.6–15.6(17.8)	11.7	(4.2)4.8–8.7(8.8)	6.48	20
TAAM 189353	(53.8)61.7–88.2(96.3)	71.0	(7.0)7.6–17.2(18.7)	11.0	(3.8)4.7–9.9(10.5)	6.85	20
<i>H. rimosa</i>	(50.2)53.3–130.5(144.3)	74.6	(6.6)6.8–18.0(18.2)	10.3	(4.4)5.1–12.1(12.7)	7.41	100
Spirin 5060	(50.5)53.3–73.0(76.0)	62.5	(6.6)6.7–10.5(12.0)	8.7	(4.4)6.0–8.9(9.6)	7.34	20
Spirin 5277	(59.7)62.1–130.5(144.3)	96.8	(8.2)8.8–18.0(18.2)	13.1	(5.0)5.3–10.7(12.7)	7.65	20
Spirin 5617	(50.2)55.2–89.5(107.5)	70.7	(7.3)7.6–11.7(12.3)	9.9	(4.9)5.5–9.8(10.3)	7.25	20
Spirin 5629	(59.0)59.2–99.8(126.2)	75.1	(8.2)8.3–15.2(15.6)	10.6	(4.5)5.1–12.1(12.5)	7.31	20
Spirin 5678	(53.2)58.2–90.3(92.2)	68.1	(6.7)6.8–10.8(11.2)	9.2	(5.5)5.8–9.4(9.9)	7.51	20
<i>H. tabacina</i>	(51.2)54.3–119.6(131.3)	78.6	(6.8)7.0–17.4(18.8)	11.4	(4.1)4.4–11.0(12.5)	7.02	380
Kotiranta 20797	(66.7)74.5–119.6(131.3)	94.6	(7.7)9.3–14.8(15.1)	12.4	(5.0)5.7–11.0(11.8)	7.81	20
Kotiranta 21006	(56.4)58.3–95.6(104.5)	78.9	(7.8)8.2–13.7(14.4)	10.6	(5.6)6.1–8.2(8.8)	7.51	20
Miettinen 7428	(56.2)62.6–89.3(95.2)	77.6	(9.5)10.3–13.7(15.6)	12.2	(4.8)4.9–8.0(9.0)	6.42	20
Kotiranta 20693	(52.3)54.3–85.5(89.8)	67.3	(8.0)8.9–14.6(18.0)	11.2	(4.2)4.5–8.0(8.7)	6.15	20
Kotiranta 25205	(51.2)60.5–83.1(112.0)	71.5	(6.8)7.0–14.0(14.4)	10.5	(5.0)5.7–11.0(11.8)	7.81	20
Kotiranta 25386a	(53.6)61.9–83.2(85.3)	70.1	(8.4)8.8–13.8(14.8)	10.7	(5.4)5.8–7.5(7.6)	6.64	20
Miettinen 17028.3	(68.7)69.0–104.5(109.9)	85.3	(9.3)10.1–12.5(12.6)	11.1	(6.0)6.8–8.7(10.1)	7.73	20
Miettinen 18168	(62.3)63.3–97.3(111.2)	76.5	(7.2)7.6–12.7(14.8)	10.0	(5.4)5.8–7.5(7.6)	7.86	20
Niemelä 2604	(69.2)70.2–98.0(109.6)	80.9	(8.5)8.6–16.5(18.0)	11.3	(4.9)5.4–8.8(10.1)	7.40	20
Niemelä 3581	(61.3)62.3–108.2(125.3)	85.0	(9.0)10.0–14.8(15.7)	11.9	(4.1)4.5–10.3(12.5)	7.35	20
Niemelä 8341	(57.2)58.3–88.6(95.7)	73.3	(7.3)7.6–13.2(14.2)	10.1	(4.8)5.2–9.5(9.8)	7.50	20
Ryvarden 14421	(73.1)74.2–91.2(101.0)	82.5	(9.2)9.8–13.7(14.2)	11.3	(5.7)5.8–8.5(9.3)	7.42	20
Spirin 5057	(61.2)63.3–102.8(104.6)	83.8	(9.7)10.4–15.4(17.2)	12.7	(4.5)4.9–8.4(10.6)	6.71	20
Spirin 5196	(49.0)55.7–79.0(83.2)	64.7	(6.0)8.3–12.0(13.2)	9.8	(5.0)5.1–8.1(8.5)	5.86	20
Spirin 5496	(63.8)69.3–88.4(108.2)	79.6	(9.8)11.1–17.4(18.8)	13.9	(4.1)4.4–7.6(9.0)	5.86	20
Spirin 6066a	(57.3)58.8–85.2(94.3)	71.2	(7.3)8.7–12.8(14.0)	10.4	(4.8)5.4–8.6(9.2)	7.01	20
Spirin 6507	(55.3)63.1–99.4(108.7)	78.8	(7.3)9.2–14.4(14.7)	12.1	(5.4)5.5–9.0(9.3)	6.59	20
Spirin 6517	(69.2)71.2–100.1(104.8)	85.0	(8.5)10.1–13.8(14.5)	11.8	(6.2)6.4–8.5(8.7)	7.24	20
Spirin 6520	(61.7)63.7–114.9(126.0)	84.1	(10.2)10.6–15.4(16.1)	13.1	(4.2)4.4–8.7(9.8)	6.49	20
<i>H. yasudai</i>	(54.8)61.4–103.7(106.0)	84.0	(8.0)10.3–16.6(17.1)	12.0	(4.0)4.1–9.2(10.3)	7.07	40
holotype	(55.2)61.4–96.5(97.6)	85.6	(9.3)10.3–16.6(17.1)	12.4	(4.0)4.1–9.2(10.3)	6.89	20
Spirin 6475	(54.8)62.2–103.7(106.0)	82.3	(8.0)10.3–14.2(16.0)	11.6	(4.9)5.0–9.2(9.5)	7.25	20

reported as for spores (Table 2). Sketches were made using a drawing tube with the exception of spores that were drawn with free hand after real measured spores. The sketches were then imported to CorelDRAW 2017 and redrawn to vector graphics. Spore statistics were produced in Microsoft Excel 2016.

We sequenced nuclear ribosomal DNA internal transcribed spacer (ITS) from 25 samples and translation elongation factor 1- α (*tef1*) from 20 samples. Sequences were produced as described in Miettinen *et al.* (2018). The resulting sequences are available in INSDC (Table 3). In addition, all publicly available

Table 3. Specimens of *Hydnoporia* and *Hymenochaete* sequenced for this study with GenBank accession numbers. Sequences marked with * derived from cultures.

Species	Collector, coll. no. (herbarium)	Country (province/state)	ITS	<i>tef1</i>
<i>Hydnoporia corrugata</i>	Jon Klepsland 11.021 (O F-247869), neotype	Norway	MK514613	MK552138
<i>Hydnoporia diffissa</i>	Otto Miettinen 17127.4 (H) *	USA (NY)	MK514598	–
	Otto Miettinen 19463 (H 7008917), holotype	USA (NC)	MK514611	MK552136
<i>Hydnoporia laricicola</i>	Viacheslav Spirin 5400 (H) *	Russia (KHA)	MK514606	MK552132
<i>Hydnoporia olivacea</i>	Otto Miettinen 16956.2 (H 7008916), epitype	USA (NY)	MK514610	–
	Otto Miettinen & Kelo Käppi 16044 (H 7005770), epitype	USA (MA)	MK514612	MK552137
<i>Hydnoporia rhododendri</i>	N. Gerhold 3 Jun 2005 (H, ex TAA 189353)	Austria	MK514593	–
	Viacheslav Spirin 6476 (H) *	Russia (PRI)	MK514599	MK552127
	Viacheslav Spirin 6450 (H) *	Russia (PRI)	MK514603	–
<i>Hydnoporia rimosa</i>	Viacheslav Spirin 5277 (H)	Russia (KHA)	MK514592	MK552122
	Viacheslav Spirin 5678 (H)	Russia (KHA)	MK514594	MK552123
	Viacheslav Spirin 6104 (H)	Russia (KHA)	MK514595	MK552124
<i>Hydnoporia tabacina</i>	Heikki Kotiranta 20797 (H)	Russia (PER)	MK514591	MK552121
	Heikki Kotiranta 25205 (H)	Russia (KK)	MK514596	MK552125
	Viacheslav Spirin 6066a (H) *	Russia (NIZ)	MK514600	MK552128
	Otto Miettinen 17028.3 (H) *	United States (NY)	MK514601	MK552129
	Otto Miettinen 22126 (H)	Finland	MK782755	MK787232
	Viacheslav Spirin 5196 (H) *	Russia (KHA)	MK514602	MK552130
	Viacheslav Spirin 6582 (H) *	Russia (KHA)	MK514604	–
	Viacheslav Spirin 6566 (H) *	Russia (KHA)	MK514605	MK552131
	Viacheslav Spirin 6520 (H) *	Russia (KHA)	MK514607	MK552133
	Viacheslav Spirin 6507 (H) *	Russia (KHA)	MK514608	MK552134
	A. M. Ainsworth & A. Lucas 17 Jan 2017 (K(M) 233332) *	UK	MK514614	MK890223
<i>Hydnoporia yasudai</i>	Viacheslav Spirin 5533 (H) *	Russia (KHA)	MK514597	MK552126
	Viacheslav Spirin 6475 (H) *	Russia (PRI)	MK514609	MK552135

sequences of *Hydnoporia* and *Hymenochaete rubiginosa* complex were included in our analyses based on BLAST and name searches: GenBank - 67 sequences; UNITE - 2 (Nilsson *et al.* 2018); BOLD - 1 (Ratnasingham & Hebert 2007).

We constructed three sequence datasets for analyses:

1. *Hydnoporia* ITS-dataset includes 94 sequences. Alignment length was 738 with 250 variable site patterns. We also analysed the same alignment after excluding fastest evolving sites (651 bp, 191 variable sites). Results were topologically identical and we report below results based on the longer alignment.
2. *Hydnoporia tef1*-dataset includes 20 sequences. After removing unalignable, ambiguous alignment positions, alignment length was 721 with 151 variable site patterns.
3. *Hymenochaete rubiginosa* ITS dataset includes 12 sequences. The closest relatives of *H. rubiginosa* s. str., determined by BLAST similarity ($\geq 94\%$) were included in the analyses. Alignment length was 660 with 71 variable site patterns.

PRANK online version at the European Bioinformatics Institute website was used for aligning sequences (Löytynoja & Goldman

2005, Cowley *et al.* 2017). Resulting alignments were refined, and alignment positions with unclear homology were excluded manually (*tef1*-dataset) using PhyDE v. 0.9971 (Müller *et al.* 2010).

Phylogenies were constructed with MrBayes v. 3.1.2 and 3.2.6 (Ronquist *et al.* 2012). Nucleotide substitution models were chosen with jModelTest v. 2.1.10 based on AIC (Darriba *et al.* 2012): GTR+I+G for the *Hydnoporia* ITS-dataset, GTR+G for the *Hydnoporia tef1*-dataset, and GTR for the *Hymenochaete rubiginosa* ITS-dataset. Analyses were run with eight chains in three parallel runs, temp = 0.1 for 5 M generations (10 M for *Hydnoporia* ITS-dataset) sampling a tree every 2 000 generations. All runs had converged to below 0.01 average standard deviation of split frequencies by the end of the run. A burn-in of 25 % was used before computing the consensus tree.

The alignments and phylograms have been deposited in TreeBASE (submission 24281). The resulting phylograms were edited in FigTree v. 1.4.3 (Rambaut 2014); since our focus was in species delimitation and in the absence of reliable rooting data, we used midpoint rooting in all cases.

Specimens examined (sequenced collections marked by asterisk):

Clavariachaete rubiginosa. **Venezuela**, Río Negro, Río Mawarinuma, 3 Feb. 1985, *Halling 4151* (NY).

Hydnoporia corrugata. **Austria**, Steiermark, Koralpe, branches, 15 Sep. 1974, Poelt (H), *Fagus sylvatica*, 20 Mar. 1977, Michelitsch (H). **Norway**, Hordaland, Bømlo, *Corylus avellana*, 24 Jul. 2011, Klepsland 11.021* (O F-247869, **neotype**). **Russia**, Kaluga Reg., Ulyanovo Dist., Kaluzhskie Zaseki Nat. Res., *C. avellana*, 1 Aug. 2013, Volobuev* (H ex LE).

Hydnoporia diffissa. **USA**, New Jersey, Gloucester Co., Newfield, hardwood, Jun. 1893, Ellis & Everhart (Fungi Columbiani #8) (H, NY), *Quercus ilicifolia* (branches), 'October' (no year indicated), Ellis (Rabenhorst-Winter Fungi Europaei #3136) (NY); New York, Essex Co., Arbutus Lake, dry branches, 22 Sep. 2013, Miettinen 17127.4* (H); North Carolina, Buncombe Co., Blue Ridge Assembly, *Rhododendron maximum*, 24 Sep. 2015, Miettinen 19463* (H); Ohio, Hocking Co., Old Man's Cave St. Park, *Fagus grandifolia*, 15 Nov. 1975, Cooke 51769 (H, O); Pennsylvania, Butler Co., Saxonburg, 18 Sep. 1939, Sumstine 12125 (NY); Indiana Co., Marion Center, 27 Sep. 1949, Henry (NY); Tennessee, Great Smoky Nat. Park, dead hardwood, 14 Jul. 2004, Ryvarden 46500 (H, O).

Hydnoporia laricicola. **Russia**, Altai, Shebalino Dist., Cherga, *Larix sibirica*, 16 Aug. 1985, Alanko 52913 (H); Karelia, Pudozh Dist., Vodlozero Nat. Park, *L. sibirica*, 22 Jun. 1991, Ahti 50083 (H); Khabarovsk Reg., Khabarovsk Dist., Malyi Kukachan, *Larix gmelinii*, 19 Aug. 2012, Spirin 5400* (H); Solnechnyi Dist., Igdomi, *L. gmelinii*, 5 Aug. 2011, Spirin 3810 (H); Verkhnebureinskii Dist., Kyvyty, *L. gmelinii*, 17 Aug. 2014, Spirin 7457 (H); Dublikan, *L. gmelinii*, 23 Aug. 2014, Spirin 7954 (H).

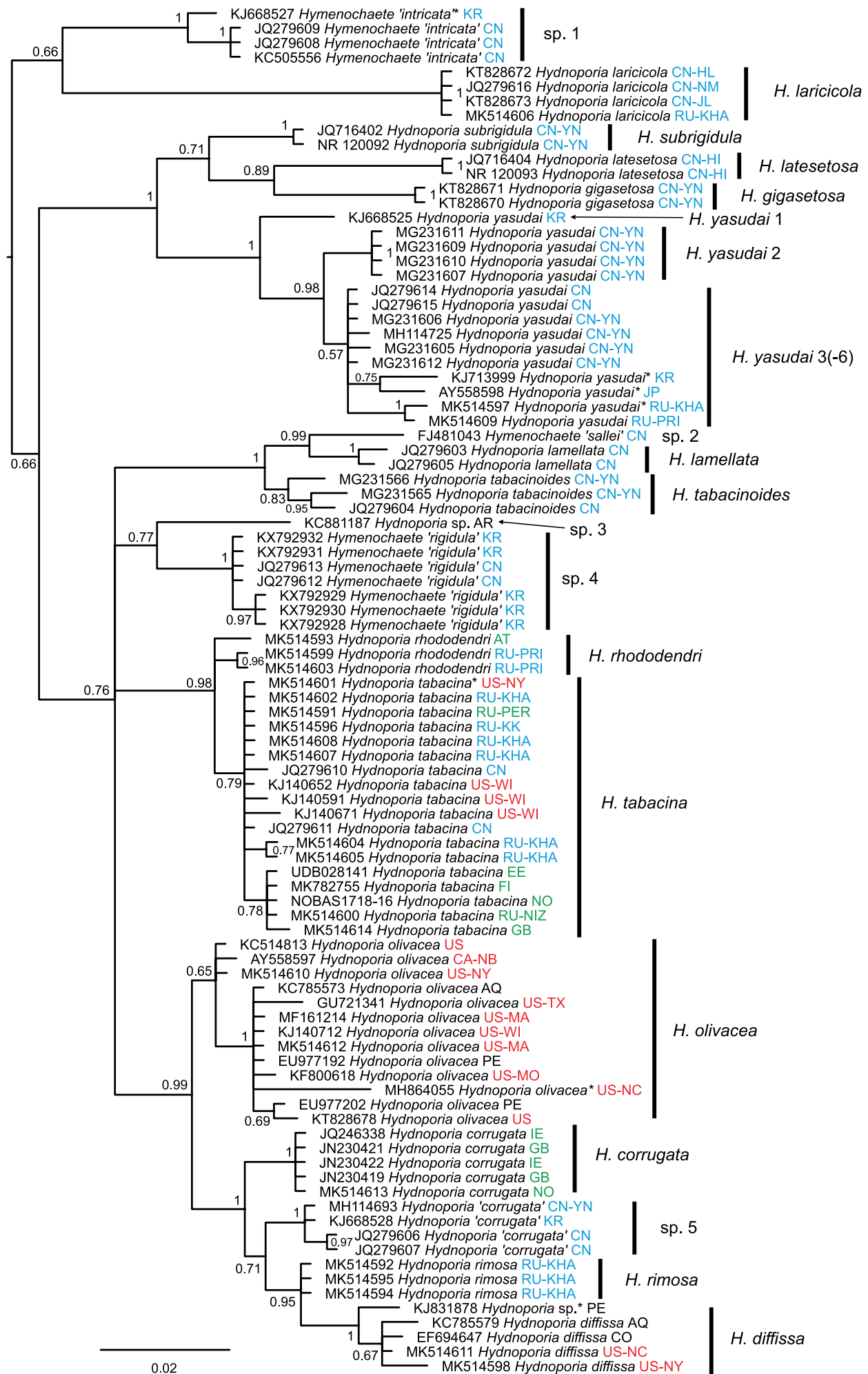
Hydnoporia olivacea. **USA**, New Jersey, Gloucester Co., Newfield, hardwood, 1874 Ellis (NY 00742784, **lectotype** of *Hymenochaete agglutinans*), Nov. 1881, Ellis (NY ex C. Roumeguère, Fungi Selecti Exsiccati #4540, **epitype** of *H. agglutinans*); New York, New York: Essex Co., Huntington Wildlife Forest, Adjidaumo flow, *Fagus grandifolia*, 18 Sep. 2013, Miettinen 16956.2* (H 7008916, **epitype** of *Thelephora episphaeria*); North Carolina, Burke Co., Salem, Schweinitz (UPS F-173549) (**lectotype** of *Sistotrema fuscescens*), the same locality, Schweinitz (UPS F-173519) (**lectotype** of *Thelephora episphaeria*); Durham/Orange Co., Eno River State Park, dicot, 2 Nov. 1997, E. Larsson 90-97* (GB 0150286); Massachusetts, Worcester, Columbus Park, hardwood, 11 Apr. 2013, Miettinen 16044 & Käppi* (H 7005770, **epitype** of *Sistotrema fuscescens*).

Hydnoporia rhododendri. **Austria**, Tyrol, Kaunertaler Gletscherstrasse, *Rhododendron ferrugineum*, 3 Jun. 2005, Gerhold* (H ex TAAM 189353, isotype?); **Russia**, Buryatia, Barguzin Dist., Shumilikha, *Rhododendron tomentosum*, 28 Aug. 2003, Ryvarden 45907 (O); Primorie Reg., Krasnoarmeiskii Dist., Valinku, *Rhododendron hypoleucum*, 28 Aug. 2013, Spirin 6450* (H); 6452 (H); 29 Aug. 2013, Spirin 6476* (H). **Sweden**, Uppland, Roslagen, *Calluna vulgaris* (or *Empetrum nigrum*), 16 Jul. 1906, Starbäck (H). **Switzerland**, Graubünden, St. Moritz, *R. ferrugineum*, Aug. 1882, Winter (H ex Rabenhorst-Winter Fungi Europaei #2932, as *Stereum tabacinum*).

Hydnoporia rimosa. **Japan**, Tōhoku, Sendai, 24 Oct. 1920, Yasuda (TNS F-203210, lectotype). **Russia**, Khabarovsk Reg., Khabarovsk Dist., Malyi Niran, *Corylus mandshurica*, 8 Aug. 2012, Spirin 5060 (H); Ulika, *C. mandshurica*, 14 Aug. 2012, Spirin 5277* (H); Ulun, *Ulmus japonica*, *Rhododendron dauricum*, *Syringa amurensis*, 26 Aug. 2012, Spirin 5617, 5629, 5678* (H); Komsomolsk Dist., Boktor, *C. mandshurica*, 18 Aug. 2013, Spirin 6104* (H) (basidiocarps and sterile stage); Solnechnyi Dist., Igdomi, *Quercus mongolica*, 7 Aug. 2011, Spirin 3952 (H); *Duschekia fruticosa*, 2 Sep. 2016, Spirin 10797 (H); Sonakh, *Q. mongolica*, 15 Aug. 2014, Spirin 7294 (H).

Hydnoporia tabacina. **Canada**, Québec Nordique, Poste-de-la-Baleine, *Alnus crispa*, 29 Jul. 1982, Niemelä 2569 (H); 10 Aug 1982, Niemelä 2720 (H); *Salix*, 31 Jul. 1982, Niemelä 2604 (H). **China**, Jilin Prov., Antu Co., Huang Song Pu, *Acer*, 28 Aug. 2005, Miettinen 10618.2 (H). **Estonia**, Jõgevamaa, Imukvere, *Picea abies*, 22 Sep. 1956, Parmasto (Mycotheca Estonica 1: 7, 1957) (H ex TAAM); Tartumaa, Kastre, *P. abies*, 20 Jun. 1930, Lepik (Fungi Estonici Exsiccati 1: 9, 1931) (H); Valgamaa, Paluperä, Käpa, *Corylus avellana*, 13 Sep. 2012, Kotiranta 25386a (H). **Finland**, Varsinais-Suomi, Tammisaari, Lökudden Nat. Res., *Ribes alpinum*, 1 Sep. 2004, Kotiranta 20693 (H); Uusimaa, Helsinki, Viikki, *C. avellana*, 18 Mar. 2014, Miettinen 18168* (H); Veräjämäki, *P. padus*, 7 Apr. 2019, Miettinen 22126* (H); Etelä-Häme: Lammi Biol. Station, *Quercus robur*, 17 Sep. 2013, Spirin 6723a (H); Untulanharju, *P. abies*, 17 Sep. 1986, Niemelä 3581 (H); Lapinjärvi, *P. abies*, 8–9 Sep. 2003, Miettinen 7428 (H); Luhanka, Sepänmäki, *Juniperus communis*, 21 Oct. 2004, Kotiranta 21006 (H); Pohjois-Savo, Enonkoski, Kolovesi Nat. Park, *Salix caprea*, 30 Sep. 2006, Niemelä 8341 (H). **Japan**, Hokkaido, Tomakomai, Iburi, *Alnus*, 20 Dec. 1904, Niidjima 706 (TNS F-200336, **isotype** of *Hymenochaete intricata*); Honshu, Kantō, Tochigi, *Larix*, 31 Oct. 1991, Ryvarden 30234 (O). **Russia**, Khabarovsk Reg., Khabarovsk Dist., Malyi Niran, *Pinus koraiensis*, 8 Aug. 2012, Spirin 5057 (H); Ulika, *Actinidia kolomikta*, 13 Aug. 2012, Spirin 5196* (H); Bolshoi Khechtsir, *Picea ajanensis*, 2–3 Sep. 2013, Spirin 6517, 6582* (H); *C. mandshurica*, 2 Sep. 2013, Spirin 6520* (H); *Acer ukurunduense*, 3 Sep. 2013, Spirin 6566* (H); Levyi Ulun, *R. dauricum*, 22 Aug. 2012, Spirin 5496 (H); Solnechnyi Dist., Igdomi, *Alnus hirsuta*, 4 Aug. 2011, Spirin 3776, 3780 (H); Khakassia, Abakan Dist., Erkagi, *Salix viminalis*, 15 Aug. 2011, Kotiranta 25205* (H); Krasnoyarsk Reg., Krasnoyarsk, Stolby Nat. Res., *Abies sibirica*, 13 Aug. 1980, Parmasto (O ex TAAM 102904); Nizhny Novgorod Reg., Lukoyanov Dist., Sanki, *C. avellana*, 10 Aug. 2013, Spirin 6066a* (H); Razino, *Pinus sylvestris*, 8 Aug. 1998, Spirin (H ex LE 211323); Perm Reg., Krasnovisherskii Dist., Kvarkush, *S. caprea*, 6 Aug. 2005, Kotiranta 20797* (H); Primorie Reg., Krasnoarmeiskii Dist., Valinku, *A. ukurunduense*, 27 Aug. 2013, Spirin 6409 (H); *Picea koreana*, 29 Aug. 2013, Spirin 6507* (H). **Sweden**, Skåne, Fries (UPS F-175737, **lectotype** of *Thelephora tabacina*); Uppland, Uppsala, Silva Nosten, *P. abies*, 16 May 1929, Lundell (H ex Fungi Suecici #487). **UK**, England, South Hampshire, New Forest, *Salix*, 17 Jan. 2017, Ainsworth & Lucas* (K(M) 233332). **USA**, Minnesota, Clearwater Co., Itasca, 16 Sep. 1977, Ryvarden 14421 (H, O); New York, Tully, *Fagus*, 10 Aug. 1963, Larsen 320 (H); New York, Essex Co., Catlin Lake, deciduous

Fig. 2. Phylogram of *Hydnoporia* nrDNA ITS sequences. Bayesian consensus tree with midpoint rooting. Numbers denote posterior probabilities. Two-letter codes after species names denote country, followed by the province of origin (ISO 3166). Asian specimens have been coloured blue, European green and North American red. Sequences with the accession number starting with "MK" have been produced for this study, the rest are from public sources. Asterisk (*) denotes specimens that may represent separate species within the annotated lineages.



tree, 19 Sep. 2013, *Miettinen 17028.3** (H); North Carolina, Swain Co., Great Smokey Mtns NP, Clingmans Dome, *Abies fraseri*, 1 Oct. 2015, *Miettinen 19630* (H); dicot, *Miettinen 19631* (H).

Hydnoporia yasudai. **Japan**, Tokyo, Minami-Tama Gun, Sainokami Goryochi, *Abies firma* (dry branches), 10 Oct. 1939, *Imazeki* (TNS F-207357); Shiga Pref., Kutsuki, *Pinus*, 3 Nov. 1991, *Hattori* (H ex O 14614). **Russia**, Khabarovsk Reg., Khabarovsk Dist., Levyi Ulun, *Pinus pumila* (dry branches), 23 Aug. 2012, *Spirin 5533** (H); Solnechnyi Dist., Igdomi, *P. pumila*, 2 Sep. 2016, *Spirin 10812* (H); Primorie Reg., Khasan Dist., Kedrovaya Pad' Nat. Res., *Abies holophylla*, 22 Jul. 1985, *Parmasto* (H ex TAAM 106187); Krasnoarmeiskii Dist., Valinku, *P. pumila* (dry branches), 29 Aug. 2013, *Spirin 6475** (H).

Hymenochaete allantospora. **Mexico**, Veracruz, Xalapa-Coatepec, Santa Inés, 29 Mar. 1990, *Bandala* (TAAM 171364, **holotype**).

Hymenochaete iodina. **Brazil**, Pernacumbo, Cabo de Santo Agostinho, Mata de Gurjaú, Jul. 2001, *Gibertoni 365* (O F-917605); Caruaru, Parque Ecológico Municipal Vasconcelos Sobrinho, Oct. 2000, *Cáceres & Lücking 396* (O F-917951).

Hymenochaete saepiaria. **Australia**, New South Wales, Sydney, no date, *Clealand* (Lloyd's herb. #24124) (BPI US0325520, **lectotype**).

Hymenochaete rubiginosa. **Russia**, Nizhny Novgorod Reg., Lukoyanov Dist., Panzelka, *Quercus robur*, 6 Aug. 2014, *Spirin 7134* (H). **Sweden**, Småland, Femsjö, *Fries* (UPS F-175700, **lectotype** of *Thelephora rubiginosa*). **Switzerland**, Basel-land, Liestal, Wildenstein, *Quercus* (?), 14 Jun. 2009, *Miettinen 13667.2** (H). **USA**, Massachusetts, Worcester, Wachusett Mtn. State Reservation, *Quercus*, 28 Oct. 2014, *Miettinen 19066** (H); Oklahoma, Payne Co., Carl Blackwell Lake, *Quercus*, 8 Nov. 1979, *Cooke 56530* (H ex O F14563); Tennessee, Cocke Co., Cosbey Creek, *Quercus* (?), 2 Oct. 2015, *Miettinen 19659.2* (H); Sevier Co., Great Smokey Mtns., Ramsey Cascade Trail, *Quercus*, 30 Sep. 2015, *Miettinen 19593** (H).

RESULTS

Our phylogenetic analyses focused on species delimitation within the genus *Hydnoporia* (= *Pseudochaete*, *Hymenochaetopsis*). We included all publicly available *Hydnoporia* ITS sequences in the analysis, altogether 94. According to our interpretation, ITS variation indicates presence of at least 20 species, but possibly up to 27 species (Fig. 2). Two of the sequences may be contaminants (KC785573, KC785579), supposedly originating from soil in a barren Antarctic cave (Connell & Staudigel 2013), while representing common North American species (*Hydnoporia diffissa*, *H. olivacea*).

Our estimate of the species number is based on combination of two approaches: extrapolating from sequence data of our own specimens, where morphological differences are documented, and comparing sequence differences within and between clades (Fig. 2). All except two of the clades we have annotated as species contain several ITS sequences. ITS differences vary, but generally intraspecific variation is 0–3 bp (< 0.5%), while sister species show differences above 5 bp (> 0.8%). However,

the difference between *H. tabacina* and its morphologically and ecologically distinct sister species *H. rhododendri* is merely 2 bp (0.3 %).

In contrast, differences between *tef1* sequences (primer pair 983-G) are much larger between species, for instance 14 bp (1.7 %) between the aforementioned *H. tabacina* vs. *H. rhododendri* case (Fig. 3). The *tef1* dataset supports separation of Far East *H. rhododendri* from the rest of *H. tabacina*, as well as all other divisions visible between species in the ITS dataset. *Hydnoporia yasudai*, in particular, would deserve further study - according to ITS data at least three species are present in East Asia in this complex, but it is unclear which of them is the real *H. yasudai*.

While we have indicated the presence of 20 or more species based on the ITS dataset (Fig. 2), we accept only 14 formally described *Hydnoporia* species in this paper. Clearly more research effort is needed to sort out species names and true diversity in *Hydnoporia*. The species diversity of *Hydnoporia* seems to be high in East Asia compared to other temperate areas, although skewed sampling likely explains this pattern partially.

Taxonomy

Hydnoporia Murrill, *North Am. Fl.* 9: 3. 1907.

Type species: Sistotrema fuscescens Schwein. [current name *Hydnoporia olivacea* (Schwein.) Teixeira].

Basidiocarps brown, resupinate to effused-reflexed with smooth to hydroid hymenophore. *Hyphal system* dimitic with intermediary hyphae or setal hyphae, and simple septa. *Setae* very large (up to 140 × 18 µm), pointed, born deep in trama. *Basidia* narrow, tightly packed, narrowly clavate. *Basidiospores* curved cylindrical or allantoid, small- to middle-sized, 4–7 × 1–2.5 µm. Some species are known to produce compact mycelial mats infecting living branches.

Notes: Description and typification by Murrill (1907) leaves no doubt that he had in mind the species commonly known as *Hydnochaete olivacea* when describing the monotypic genus. *Hydnoporia* can be morphologically divided in two groups: effused-reflexed species (*H. tabacina* coll.) and resupinate (*H. corrugata* coll.). This division is not supported by our phylogeny (Fig. 2). Resupinate species are found in the *H. corrugata* - *H. olivacea* clade only, but pileate species are otherwise present in several clades separate from the *H. tabacina* complex.

When describing *Hymenochaetopsis* (i.e. *Hydnoporia*), Yang et al. (2016) made no serious attempt to define the genus morphologically in comparison to *Hymenochaete*. They listed one possible character to separate the genera: basidiospores, which are narrowly and shortly cylindrical with a maximum size of 7 × 2.5 µm in *Hymenochaetopsis*.

While spore size and shape are useful characters, they are not alone sufficient for genus identification. All *Hydnoporia* species have relatively small cylindrical, slightly curved basidiospores, but so do some *Hymenochaete* spp. For instance, *Hymenochaete fuliginosa* and *Hydnoporia corrugata* have very similar cylindrical basidiospores. Other members of *Hymenochaete* with small cylindrical spores include *Hymenochaete nanospora* (sequenced in Wagner & Fischer 2002, He & Dai 2012) and *Hymenochaete pinnatifida* (Wagner & Fischer 2002, Parmasto et al. 2014) to mention a few further examples. Morphological differences exist, however, and are discussed below under *Hymenochaete*.

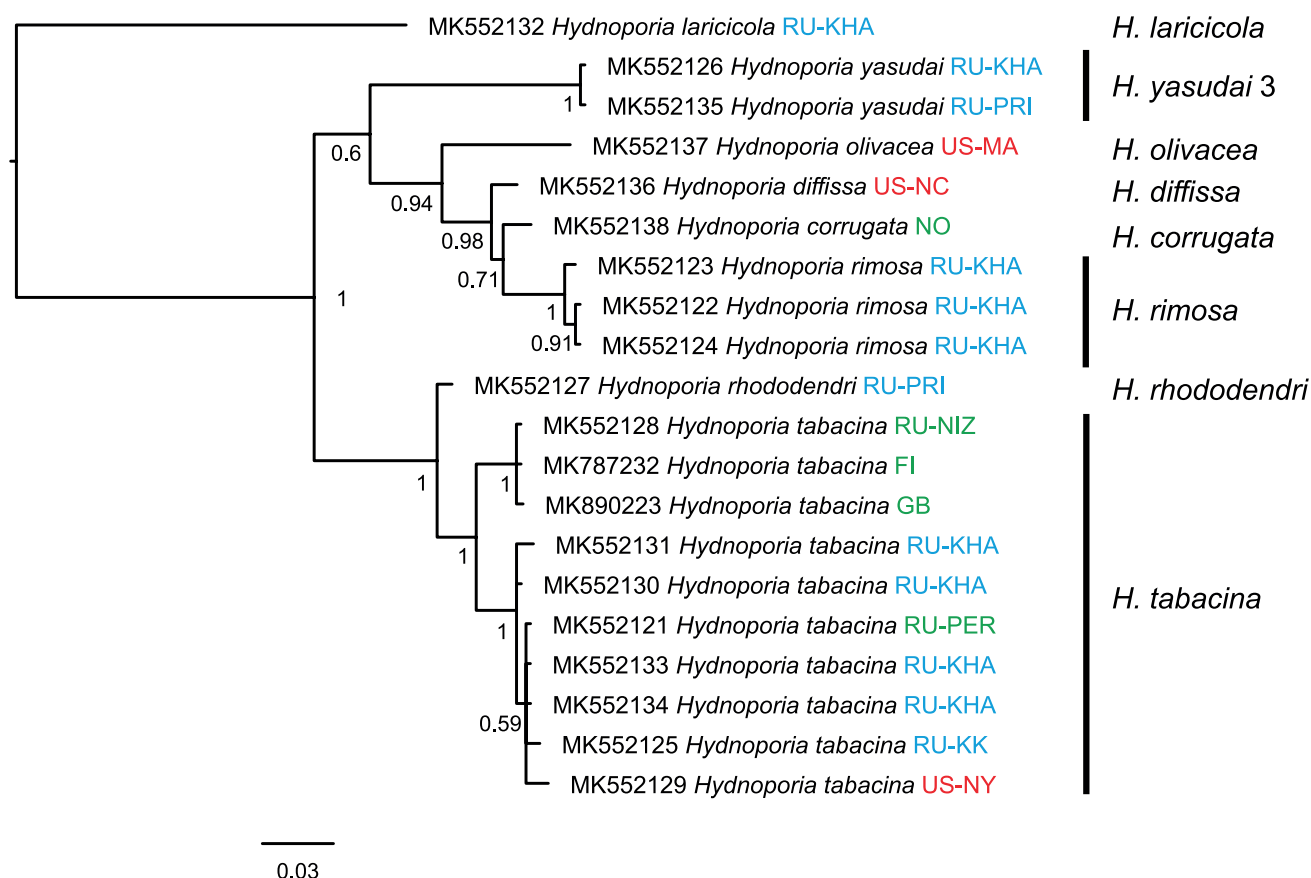


Fig. 3. Phylogram of *Hydnoporia* nrDNA *tef1* sequences. Bayesian consensus tree with midpoint rooting. Numbers denote posterior probabilities. Two-letter codes after species names denote country, followed by the province of origin (ISO 3166). Asian specimens have been coloured blue, European green and North American red.

We base our species concept in *Hydnoporia* on sequence data from two markers, indicating lack of gene flow. When defining species, sequence data are used in combination with geographic range, host specificity, basidiocarp morphology, and microscopic characters (setae and spore shape and size in particular). Species delimitation without DNA sequencing is possible with the combination of the above-mentioned traits (Table 4), but in many cases requires careful study under the microscope. As discussed under *H. tabacina*, it may be that morphologically cryptic species are found in the genus, but this needs to be confirmed in future studies.

Eleven generic names have been used for hymenochaete-like fungi in addition to *Hydnoporia*. Eight of them belong to the *Hymenochaete* clade (*Cerrenella*, *Cyclomyces*, *Cycloporrellus*, *Dichochaete*, *Hydnochaete*, *Hymenochaete*, *Hymenochaetella*, *Stiptochaete*), and two to the *Hydnoporia* clade (*Pseudochaete*, *Hymenochaetopsis*). One genus, *Clavariachaete*, has not been sequenced. Below we summarize information for these genera.

Cerrenella Murrill, Bull. Torrey Bot. Cl. **32**: 361. 1905.

Type species: *Irpex tabacinus* Berk. & Curt. (current name *Hymenochaete odontoides* S.H. He & Y.C. Dai)

He & Dai (2012) transferred the type species to *Hymenochaete* technically, based on sequences of Chinese material while the type originates from South Carolina. Authors of their *nomen novum* were incorrectly ascribed in the original paper (reference to Berk. & M.A. Curtis ex Fr. should not be used), but such a technical error does not affect validity of the new name (ICN

Art. 41.6). Based on the description of Ryvarden (1982a) and our experience it is clear that this transfer was justified.

Clavariachaete Corner, *Annals of Botany Memoirs* **1**: 689. 1950.

Type species: *Clavariachaete rubiginosa* (Berk. & M.A. Curtis ex Cooke) Corner.

When Corner (1950) described *Clavariachaete*, he mentioned confusingly that the genus is based on the bogus *Clavariachaete* McGinty, typified by *C. peckoltii*, while at the same time specifying *C. rubiginosum* as the generic type (page 689). The McGinty names by Lloyd are generally considered invalid, a filament of Lloyd's sense of humour (Stevenson & Cash 1936). Thus, the valid description is that of Corner, and the valid generic type is *C. rubiginosa*, as generally acknowledged.

Clavariachaete reminds morphologically quite closely *Hymenochaete* and does not fit *Hydnoporia*: regular, middle-sized setae, unambiguously monomitic hyphal structure and broad ellipsoid spores (Parmasto 2010). We are confident that *Clavariachaete* is not congeneric with *Hydnoporia*, but whether the genus is a taxonomic synonym of *Hymenochaete* or a well-defined genus of its own, remains to be seen.

Parmasto (2010) described a new family, *Clavariachaetaceae*, based on this genus. Whereas the genus *Clavariachaete* may stand time, we do not think that the family is justified. *Clavariachaete* fits very well in the *Hymenochaetaceae*.

Cyclomyces Fr., *Linnea* **5**: 512. 1830.

Type species: *Cyclomyces fuscus* Fr. [current name *Hymenochaete campylopore* (Mont.) Spirin & Miettinen].

Table 4. Morphological comparison of northern temperate *Hydnoporia* species with a smooth hymenophore.

Species	Substrates / distribution	Macroscopic characters	Subhymenial / tramal setae	Basidiospores
<i>H. corrugata</i>	Dead angiosperm branches; Europe	Resupinate, sterile stage absent; hymenial surface grey to pale brown, margin slightly lighter or concolorous	Sharp- to blunt-pointed, 52–86 × 7–14, L=66.8, W=9.8, Q=7.00	Cylindrical, 4.1–5.5 × 1.6–1.8, L=4.76, W=1.70, Q=2.65–2.90
<i>H. diffissa</i>	Dead or living angiosperm branches; North America (Northeast)	Resupinate, sterile stage sometimes present; hymenial surface grey to pale brown, margin slightly darker or concolorous	Sharp- to blunt-pointed, 51–73 × 7–11.5, L=75.8, W=11.0, Q=7.10	Cylindrical, 4.2–7.3 × 1.7–2.2, L=5.28, W=1.92, Q=2.50–3.00
<i>H. laricicola</i>	<i>Larix</i> spp. (bark and branches); northern Eurasia	Effused-reflexed; hymenial surface dark grey to chocolate-brown, margin concolorous	Blunt-pointed, 31–69 × 6–12, L=43.9, W=8.1, Q=5.41	Cylindrical, 4.3–6.8 × 1.7–2.1, L=5.27, W=1.91, Q=2.56–2.99
<i>H. rhododendri</i>	<i>Ericaceae</i> ; boreal Eurasia	Effused-reflexed; hymenial surface pale brown, margin slightly lighter or concolorous	Rather sharp-pointed, 56–95 × 6–17, L=71.2, W=10.5, Q=7.19	Allantoid, 3.9–5.2 × 1.2–1.6, L=4.56, W=1.33, Q=3.31–3.51
<i>H. rimosa</i>	Dead or living angiosperm branches; temperate East Asia	Resupinate, sterile stage sometimes present; hymenial surface grey to pale brown, margin slightly lighter or concolorous	Rather blunt-pointed, 53–131 × 7–18, L=74.6, W=10.3, Q=7.41	Cylindrical, 4.2–6.3 × 1.8–2.3, L=5.22, W=1.99, Q=2.47–2.78
<i>H. tabacina</i>	Angiosperms, rarely gymnosperms; holarctic	Effused-reflexed; hymenial surface greyish brown to brown, margin slightly lighter or concolorous	Rather sharp-pointed, 54–120 × 7–17, L=78.6, W=11.4, Q=7.02	Cylindrical, 4.1–6.2 × 1.5–2.1, L=4.93, W=1.81, Q=2.40–2.99
<i>H. yasudai</i>	<i>Pinus</i> spp. (dead branches), rarely other gymnosperms; boreal/temperate East Asia	Effused-reflexed; hymenial surface bright ferruginous-brown, margin slightly lighter or concolorous	Sharp-pointed, 61–104 × 10–17, L=84.0, W=12.0, Q=7.07	Cylindrical, 4.4–6.1 × 2.0–2.3, L=5.28, W=2.09, Q=2.53

All the species sequenced thus far, including the type species, belong to the *Hymenochaete* clade with the exception of *C. lamellatus* (Wagner & Fischer 2002, He & Dai 2012, Parmasto *et al.* 2014). While transferring *C. fuscus* to *Hymenochaete*, Wagner & Fisher (2002) changed its name to *Hymenochaete cyclolamellata* T. Wagner & M. Fisch, to avoid homonymy with *Hymenochaete fusca* P. Karst. However, they overlooked *Polyporus campyloporus* Mont., considered a synonym of *C. fuscus* (Ryvarden 1982b), which can serve as a basionym if *C. fuscus* is unavailable. *Cyclomyces tabacinus* presents a similar case: the epithet is not available in *Hymenochaete* and it was replaced with *Hymenochaete porioides* *nom. nov.* by Wagner & Fischer (2002). They overlooked that *Polyporus microcyclus* Zipp. ex Lév. is available as a taxonomic synonym (Ryvarden 1981), and its epithet is not previously occupied in *Hymenochaete*. Hence new combinations:

Hymenochaete campylopora (Mont.) Spirin & Miettinen, **comb. nov.** MB830586.

Basionym: *Polyporus campyloporus* Mont., *Ann. Sci. Nat., Bot., sér. 4*, **1**: 132. 1854.

Synonyms: *Cyclomyces fuscus* Kunze ex Fr., *Hymenochaete cyclolamellata* T. Wagner & M. Fisch.

Hymenochaete microcycla (Zipp. ex Lév.) Spirin & Miettinen, **comb. nov.** MB830587.

Basionym: *Polyporus microcyclus* Zipp. ex Lév., *Ann. Sci. Nat., Bot., sér. 3*, **2**: 188. 1844.

Synonyms: *Cyclomyces tabacinus* (Mont.) Pat., *Hymenochaete porioides* T. Wagner & M. Fisch.

Cycloporcellus Murr., *Bull. Torrey Bot. Cl.* **34**: 468. 1907.

Type species: *Polyporus iodinus* Mont. [syn. *Cycloporcellus iodinus* (Mont.) Murrill, *Cyclomyces iodinus* (Mont.) Pat., current name *Hymenochaete iodina* (Mont.) Baltazar & Gibertoni].

Before the revision of *Hymenochaete*, *Cycloporcellus* was considered a taxonomic synonym of *Cyclomyces* (Ryvarden 1991). The type species *H. iodina* is morphologically very close to sequenced species of other poroid *Hymenochaete* such as *H. campylopora* (= *Cyclomyces fuscus*) and *H. microcycla* (= *Cyclomyces tabacinus*) (Gomes-Silva *et al.* 2012). It is clear that *H. iodina* belongs to the *Hymenochaete* clade and *Cycloporcellus* should be considered a taxonomic synonym of *Hymenochaete* for now.

Dichochoete Parmasto, *Folia Crypt. Estonica* **37**: 56. 2000.

Type species: *Thelephora setosa* Sw. [syn. *Dichochoete setosa* (Sw.) Parmasto, current name *Hymenochaete resupinata* (Sw.) Parmasto].

Parmasto (2000) described this genus for two *Hymenochaete* species (the type *H. setosa* and *H. ceratophora*) based on dichohyphidia. Dichohyphidia are found and even more conspicuous in other members of *Hymenochaete* such as *H. cruenta* (Léger 1998). The type species of *Dichochoete* (under the name *Hymenochaete resupinata*) as well as *H. cruenta* have been shown to belong to *Hymenochaete* by molecular means (Parmasto *et al.* 2014).

Hydnochaete Bres, *Hedwigia* **35**: 287. 1896.

Type species: *Hydnochaete badia* Bres. [syn. *Hydnochaete peroxydata* (Berk. ex Cooke) Dennis, current name *Hymenochaete peroxydata* (Berk. ex Cooke) Baltazar *et al.*].

The type species has been sequenced and belongs to *Hymenochaete* (Baltazar *et al.* 2014). Also *H. asetosa*, *H. duportii*, *H. japonica*, *H. paucisetigera*, *H. resupinata* and *H. tabacina* (= *Hymenochaete odontoides*) belong to *Hymenochaete* (Wagner & Fischer 2002, He & Dai 2012, Parmasto *et al.* 2014) but *Hydnochaete tabacinoides* has been shown to belong to

Table 5. Comparison of general morphological differences between *Hydnoporia* and *Hymenochaete*.

Characters	<i>Hymenochaete</i>	<i>Hydnoporia</i>
Hyphal system	Monomitic or dimitic with true skeletal hyphae	Resupinate species: monomitic with sclerified basal hyphae; effused-reflexed species: dimitic with less distinct differences between hyphal types, often with setal hyphae
Setae	Rather stable in length and width, originating mostly from subhymenium or lower trama	Variable in size and mostly very wide, originating at different levels of trama
Subhymenium	Rather loosely arranged, often short and inflated cells	Densely arranged and only slightly inflated cells
Basidia	Suburniform with a clear medial constriction	Narrowly clavate or sinuous, not constricted
Spores	Broadly ellipsoid to cylindrical, rarely allantoid	Cylindrical to allantoid and often glued together
Mycelial mats infecting adjacent substrate	Absent	Present in some if not all species (Stenlid & Holmer 1991, Parmasto 2001, our observations)

Pseudochaete (= *Hydnoporia* in current sense; He & Dai 2012). Based on the type material of *Hydnochaete saepiaria* we have studied, the species belongs to *Hymenochaete*.

Hymenochaete saepiaria (Lloyd) Spirin & Miettinen, **comb. nov.** MB830588.

Basionym: *Irpex saepiarius* Lloyd, *Mycol. Writings* 5(48): 682. 1917.

Hymenochaete Lév., *Ann. Sci. Nat., Bot., sér. 3*, 5: 150. 1846.

Type species: *Helvella rubiginosa* Dicks. [current name *Hymenochaete rubiginosa* (Dicks.) Lév.]

The name is conserved against *Cyclomyces* Kunze ex Fr and *Hymenochaeta* P. Beauv. ex T. Lestib. (*Angiospermae*) (ICN Appendix III).

Parmasto *et al.* (2014) demonstrated that the type species of *Hymenochaete* and *Hydnoporia* (as *Pseudochaete olivacea*) belong to distinct clades separated by several polypore genera phylogenetically. Since Wagner & Fischer (2002) *Hymenochaete* has been expanded considerably to include also hydroid and

poroid taxa that belong to a well-supported clade in DNA-based analyses, while excluding species of the *Hydnoporia* clade. We discuss *Hymenochaete* here in that wide sense.

Hydnoporia and *Hymenochaete* are morphologically very similar. Differences are listed in Table 5. As can be expected in the case of such a large and variable genus as *Hymenochaete*, not all characters work for each single species. However, combination of characters (Table 5) does work, and with careful observations, it is possible to separate *Hydnoporia* and *Hymenochaete* morphologically.

The typification of the generic type, *H. rubiginosa*, requires clarification. *Hymenochaete rubiginosa* has been conserved as the generic type of *Hymenochaete* (ICN Appendix III). However, the original English material of *Helvella rubiginosa* Dicks. which could be used for the species typification does not exist (Parmasto 2001). Job (1990) selected Lloyd's collection from Ohio as a neotype of *H. rubiginosa*, but we disagree with his decision. According to our analysis of ITS sequences, the current concept of *H. rubiginosa* covers probably at least four species: European (*i.e.* *H. rubiginosa* s. str.), two unnamed sibling species from North America, and one from East Asia (Fig. 4). The type

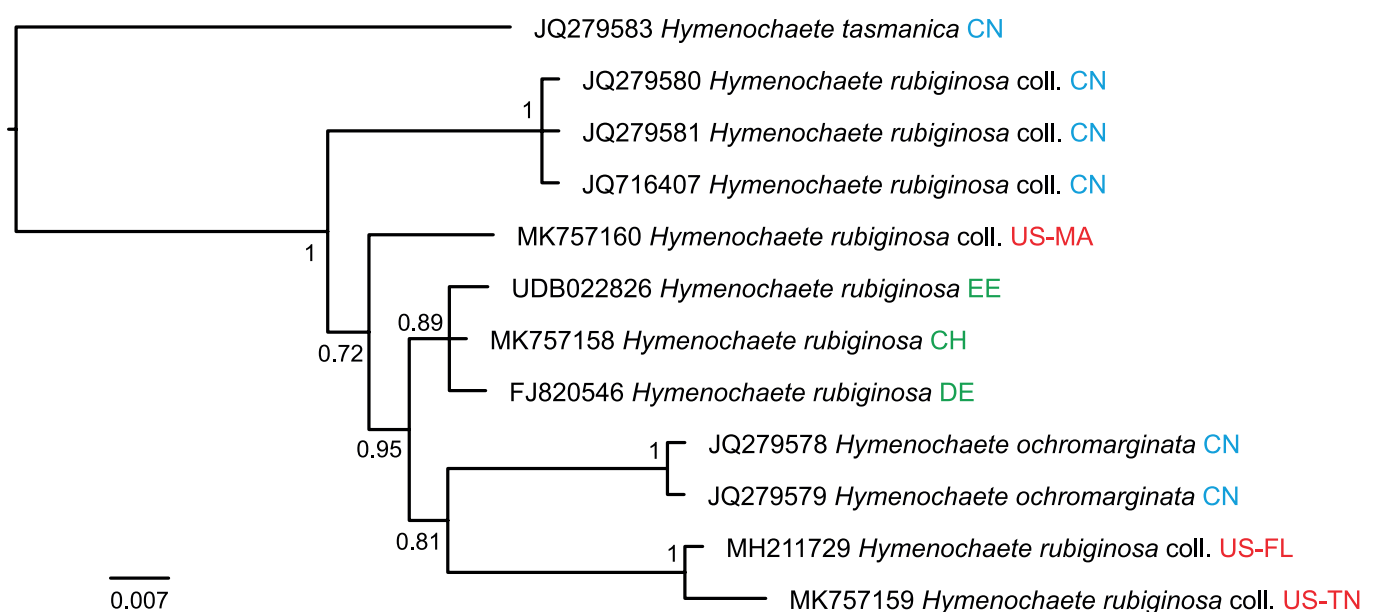


Fig. 4. Phylogram of *Hymenochaete rubiginosa* and closely related species. Bayesian consensus tree based on nrDNA ITS sequences with midpoint rooting. Numbers denote posterior probabilities. Two-letter codes after species names denote country, followed by the province of origin (ISO 3166). Asian specimens have been coloured blue, European green and North American red. Sequences with the accession number starting with “MK” have been produced for this study, the rest are from public sources.

of *H. rubiginosa* should have been designated from European material.

For this reason, we suggest to typify *H. rubiginosa* with an authentic specimen from the Fries herbarium in Uppsala: Sweden. Småland: Femsjö, Fries (UPS F-175700, **lectotype** of *Helvella rubiginosa* Dicks. designated here, MBT386587). This specimen was with high likelihood collected prior to 1821 when the sanctioning work *Systema Mycologicum* was published (Fries 1821) and is suitable as a lectotype (ICN Art. 9.3). Our reasoning is as follows: Fries used the name *Stereum rubiginosum* for this species in Fries (1818: 274), and this is how Fries has labelled the lectotype (his handwriting is visible). In *Systema Mycologicum* (Fries 1821) he switched to the name *Thelephora rubiginosa* for this species. Thus, the lectotype predates the sanctioning and is the only authentic specimen of this species in Fries's herbarium.

The four relatives of *H. rubiginosa* in North America and East Asia need other names in the future. For the time being they can be labelled *H. rubiginosa* coll. One of them is labelled *H. ochromarginata* (He & Dai 2012), but because *H. ochromarginata* was described from Africa, its applicability to Chinese material should be critically assessed.

Hymenochaetella P. Karst., *Bidrag till Kännedom av Finlands Natur och Folk* **48**: 428. 1889.

Type species: *Hymenochaetella arida* P. Karst, chosen by Cooke (1953) [current name *Hymenochaete cinnamomea* (Pers.) Bres.].

The type species belongs to *Hymenochaete*, as shown by Wagner & Fischer (2002) and confirmed by subsequent authors.

Hymenochaetopsis S.H. He & Jiao Yang, *Mycol. Prog.* **15**: 2. 2016.

Type species: *Auricularia tabacina* Sowerby [syn. *Hymenochaetopsis tabacina* (Sowerby) S.H. He & Jiao Yang, current name *Hydnoporia tabacina* (Sowerby) Spirin *et al.*].

Nomen novum for *Pseudochaete*, a taxonomic synonym of *Hydnoporia*.

Pseudochaete T. Wagner & M. Fischer, *Mycol. Prog.* **1**: 100. 2002.

Type species: *Auricularia tabacina* Sowerby [syn. *Pseudochaete tabacina* (Sowerby) T. Wagner & M. Fisch., current name *Hydnoporia tabacina* (Sowerby) Spirin *et al.*].

Illegitimate name due to ICN Art. 53.1 and *Pseudochaete* W. West & G.S. West 1903. A taxonomic synonym of *Hydnoporia* as the close relation between type species was shown by Parmasto *et al.* (2014) and confirmed here.

Stipitochaete Ryvarden, *Trans. British Mycol. Soc.* **85**: 537, 1985.

Type species: *Stereum damicornis* Link. [syn. *Stipitochaete damicornis* (Link) Ryvarden, current name *Hymenochaete damicornis* (Link) Lév.].

Ryvarden (1985) described this genus for two species of *Hymenochaete* with stipitate basidiocarps. Wagner & Fischer (2002) showed that the type species belongs to *Hymenochaete*.

Accepted species

Hydnoporia corrugata (Fr. : Fr) K.H. Larss. & Spirin, **comb. nov.** MycoBank MB830589. Figs 5, 6.

Basionym: *Thelephora corrugata* Fr., *Obs. Mycol.* **1**: 134. 1815.

Typus: **Norway**, Hordaland, Bømlo, *Corylus avellana*, 59.7002°: 5.2645°, 24 Jul. 2011, Klepsland 11.021 (O F-247869) (**neotype** designated here, MBT386588).

Notes: According to our data, *H. corrugata* is a European species (described from Sweden by Fries 1815). It usually inhabits dead, still attached or recently fallen branches of deciduous trees, especially *Betula* spp., *Carpinus betulus* and *Corylus avellana*.

Hydnoporia corrugata differs from its closest relatives, North American *H. diffissa* and East Asian *H. rimosa*, by having distinctly narrower basidiospores (see Tables 1, 4). Chinese and Korean sequences labelled as '*H. corrugata*' most probably belong to a different, closely related species (Fig. 2).

Hydnoporia diffissa Spirin & Miettinen, **sp. nov.** MycoBank MB830590. Figs 5, 6.

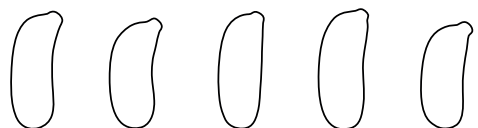
Typus: **USA**, North Carolina, Buncombe Co., Blue Ridge Assembly, 35.58356° : -82.34159° standing dead *Rhododendron maximum*, 24 Sep. 2015, Miettinen 19463 (**holotype** H 7008917).

Etymology: *Diffissum*, derived from *diffindo* (Lat., v.), named after the cracking hymenophore.

Basidiocarps perennial, effused, leathery, 0.1–0.5 mm thick, covering several cm. Margin sharply delimited and firmly attached to the substrate, first concolorous with hymenium, later ferruginous brown (in mature basidiocarps normally darker



Hydnoporia corrugata (Michelitsch s.n.)



H. diffissa (holotype)



H. laricicola (VS 5400)



H. rhododendri (VS 6450)



H. rimosa (VS 5277)

5 µm

Fig. 5. Spores of *Hydnoporia* spp.

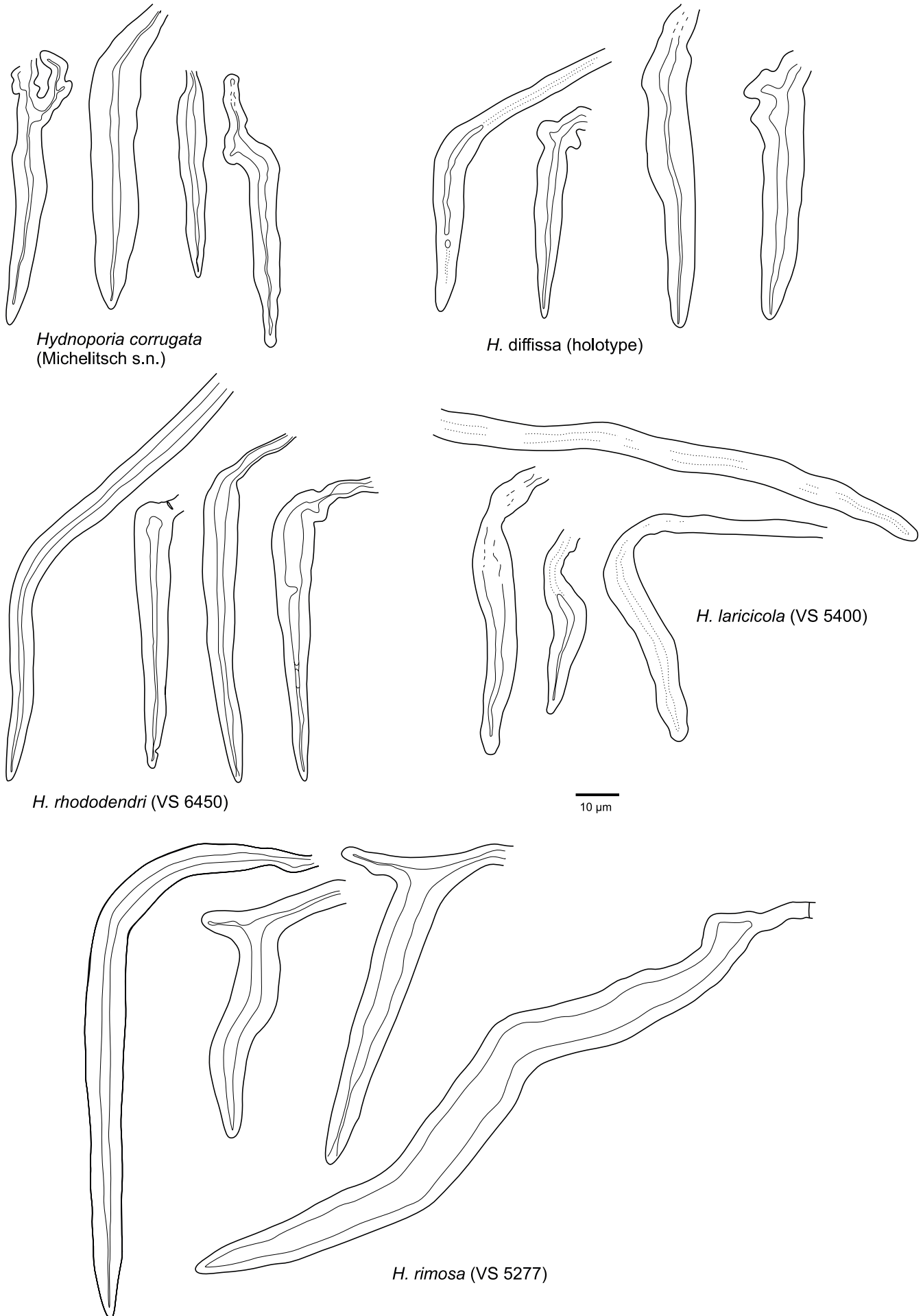


Fig. 6. Setae of *Hydnoporia* spp.

than hymenial surface). Hymenial surface even or indistinctly tuberculate, first grey to greyish ochraceous, later pale chocolate brown, in mature basidiocarps strongly rimose. Sterile patches and films bright ferruginous brown, rather small-sized, compact, associated with basidiocarps or growing solitarily. *Section*: Subiculum poorly visible, dark brown to almost black, about 20 µm thick; trama cream coloured to pale ochraceous, 30–50 µm thick; hymenium / subhymenium grey to pale brown, 30–40 µm thick, with dark coloured, mostly embedded setae. *Hyphal system* monomitic though appearing dimitic; hyphae with simple septa. Setal hyphae present in sterile films and in basal parts of senescent basidiocarps, sharp- to blunt-pointed, very thick-walled, lateral or pleural, brown, up to 170 × 12 µm. Skeletal-like hyphae often present in subiculum and lowermost parts of trama, brownish to dark-brown, occasionally branched and septate, 2–3.5 µm in diam. Generative hyphae mostly with thickened walls, in sterile films yellowish to brownish, 2–4.5 µm in diam, irregularly arranged to subparallel; in subicular layer and upper trama pale to dark brown, clearly thick-walled, more or less horizontal and parallel to the substrate, in lower trama and subhymenium hyaline to pale brown, mostly vertically arranged (2.1–)2.2–3.3(–3.6) µm diam (n = 20/1). *Tramal / hymenial setae* sharp- to blunt-pointed, normally with distinctly widened basal part, dark ferruginous brown, 47–73(–90) × 6.2–12.9 µm, L = 61 µm, W = 9.1 µm, Q = 6.82, sometimes pleural (originating from thick-walled, dark brown hyphae in upper trama) and with an apical crystalline cape, embedded or projecting up to 15–50 µm above hymenial cells, associated with simple hyaline hyphidia 1–2.5 µm in diam. *Basidia* narrowly clavate, 4-spored, 12.2–16.2(–17.2) × (2.8–)3.0–4.1 µm (n = 20/2). *Basidiospores* broadly cylindrical to cylindrical, straight to slightly curved, (4.1–)4.2–7.3(–7.8) × 1.7–2.2 µm, L = 5.28 µm, W = 1.92 µm, Q = 2.74.

Distribution and ecology: Hard angiosperm wood; our material is from the Eastern United States, but ITS sequences indicate it is present also in Colombia and Peru (Fig. 2).

Notes: Here we describe this species to encompass '*H. corrugata*' from the American Northeast. Four older names from North America had been listed among synonyms of *H. corrugata* but none of them, in our opinion, is applicable to *H. diffissa*. Three of them, *Thelephora episphaeria*, *Hymenochaete agglutinans* and *H. ambiens* are treated under *H. olivacea* (see below) while the identity of *H. insularis* is vague. Nevertheless, the white tomentose margin mentioned in the protologue (Berkeley 1873) and by Burt (1918), who studied the type material of *H. insularis*, precludes *H. diffissa*. Morphologically, *H. diffissa* is almost indistinguishable from the East Asian *H. rimosa*, except for the more variable setae in the latter species (Table 4).

Hydnoporia gigasetosa (Parmasto) Miettinen & K.H. Larss., *comb. nov.* MycoBank MB830591.

Basionym: *Hymenochaete gigasetosa* Parmasto, *Folia Cryptog Estonica* 40: 41. 2003.

Notes: Yang et al. (2016) reported this Indian species as new to China and concluded based on sequences that it belongs to *Hymenochaetopsis* (i.e. *Hydnoporia*). Their description agrees with the original description of Parmasto (2003). Large setae, allantoid basidiospores and the shape of basidia all confirm that *H. gigasetosa* belongs to *Hydnoporia*.

Hydnoporia lamellata (Y.C. Dai & Niemelä) Miettinen & K.H. Larss., *comb. nov.* MycoBank MB830592.

Basionym: *Cyclomyces lamellatus* Y.C. Dai & Niemelä, *Ann. Bot. Fenn.* 40: 384. 2003.

Notes: *Hydnoporia lamellata* is an East Asian species morphologically and phylogenetically very close to *H. tabacinoides*. Both species share all important features with other *Hydnoporia* species, and DNA data confirm their placement to the latter genus. It would be useful to compare the type of *H. tabacinoides* with sequenced material to confirm that the names *H. lamellata* and *H. tabacinoides* belong to separate species. Descriptions by Ryvarden (1982a) of *H. tabacinoides* and Dai et al. (2003) of *H. lamellata* let us believe that spore and pore size separate the two, but the description by Dai & Niemelä (2006) of *H. tabacinoides* muddles the picture. ITS data nevertheless indicates that there are two species in East Asia in this complex.

Hydnoporia laricicola (S.H. He & Jiao Yang) Spirin & Miettinen, *comb. nov.* MycoBank MB830593. Figs 5, 6.

Basionym: *Hymenochaetopsis laricicola* S.H. He & Jiao Yang, *Mycol. Prog.* 15: 3. 2016.

Basidiocarps perennial, sessile or effused-reflexed, leathery to corky, imbricate, 1–3 cm long, 0.3–0.6 mm thick, resupinate part up to 6 cm wide. Pileal surface uneven, tomentose, matt, grey, with narrow, distinct, darker zones, in older basidiocarps ferruginous brown. Pileal margin sharp, more or less even, a bit incurved in dried specimens, margin of resupinate parts sharply delimited and partly detaching from substrate, ferruginous brown. Hymenial surface even or indistinctly tuberculate, first dark grey, later chocolate-coloured, in mature basidiocarps strongly rimose. *Section*: Tomentum rather loose, grey, 50–70 µm thick; cortex well visible, dark brown to almost black, about 20 µm thick; trama more or less uniformly greyish brown, 40–60 µm thick; hymenium / subhymenium grey to rusty brown, 30–50 µm thick, with dark coloured, mostly embedded setae. Perennial basidiocarps distinctly stratified (2–4 layers divided by dark lines). *Hyphal system* dimitic; hyphae with simple septa. Setal hyphae abundant, originating deeply in trama, blunt-pointed, very thick-walled, lateral or pleural, mostly vertically arranged, dark ferruginous brown, 90–300 × 4–12 µm. Skeletal hyphae rather poorly differentiated, located in the uppermost parts of basidiocarps, dark-brown, mostly unbranched and not septate, 2–4 µm in diam. Generative hyphae mostly with thickened walls, yellowish to brownish, 2.8–4.8 µm in diam (n = 20/1), vertically and tightly arranged in tomentum, more or less horizontal and parallel in cortex and upper tramal layer, mostly vertically arranged in lower trama; subhymenium distinct, 20–30 µm thick, hyphae pale brown, with thickened walls, vertically and tightly arranged, 2.4–4.1 µm in diam (n = 10/1). *Tramal / hymenial setae* blunt-pointed, normally with widened basal part, dark ferruginous brown, 31–69(–84) × 5.3–12.2 µm, L = 44 µm, W = 8.1 µm, Q = 5.41, rarely pleural or bifurcate, some with scarce encrustation, embedded or projecting up to 15–20 µm above hymenial cells, usually associated with simple hyaline hyphidia 1–2 µm in diam. Hymenial hyphidia present, abundant, hyaline to brownish, with thickened walls and a few slight constrictions (moniliform), 1–2.5 µm diam at the apical part, embedded or projecting up to 10 µm. *Basidia* narrowly clavate, 4-spored, 15.0–22.3 × 3.1–4.1 µm (n = 20/2).

Basidiospores cylindrical, straight to slightly curved, (4.2–)4.3–6.8(–7.0) × (1.6–)1.7–2.1(–2.2) µm, L = 5.27 µm, W = 1.91 µm, Q = 2.78.

Distribution and ecology: *Hydnoporia laricicola* grows on both living and fallen trees of larch (*Larix gmelinii* and *L. sibirica*) in taiga forests of Eurasia. We have not seen material from Europe outside of Russia.

Notes: Its most striking microscopic characters are abundant setal hyphae and blunt-pointed, very short tramal and hymenial setae. *Hydnoporia tabacina* can also occur on coniferous hosts, including *Larix*, but it differs in having much larger setae (Table 2).

Hydnoporia latesetosa (S.H. He & Hai J. Li) Miettinen & K.H. Larss., **comb. nov.** MycoBank MB830594.

Basionym: *Pseudochaete latesetosa* S.H. He & Hai J. Li, *Mycol. Prog.* **12**: 333. 2013.

Notes: This species was recently described from tropical China (He & Li 2013). Large setae of varying size, setal hyphae and narrow basidiospores, as well as DNA data confirm the transfer of this species to *Hydnoporia*.

Hydnoporia lenta (G.A. Escobar ex Léger) Spirin & Miettinen, **comb. nov.** MycoBank MB830595.

Basionym: *Hymenochaete lenta* G.A. Escobar ex Léger, *Cryptog. Mycol.* **11**: 302. 1990.

Notes: *Hydnoporia lenta* was described from Costa Rica (Léger 1990), and we have not seen the type. However, the morphological description by Léger (1990, 1998) is sufficient to conclude that the species should be included in *Hydnoporia*.

Hydnoporia olivacea (Schwein.: Fr.) Teixeira, *Rev. Brasil. Bot.* **9**: 43. 1986.

Basionym: *Sistotrema olivaceum* Schwein., *Schr. Naturf. Ges. Leipzig* **1**: 101. 1822. — *Hydnum olivaceum* (Schwein.: Fr.) Fr., *Elench. Fung.* **1**: 134. 1828.

Synonyms: *Sistotrema fuscescens* Schwein., *Schr. Naturf. Ges. Leipzig* **1**: 102. 1822. **Lectotype:** USA, North Carolina, Burke Co., Salem, Schweinitz (UPS F-173549, designated here, MBT386589).

Epitype: USA, Massachusetts, Worcester, Columbus Park, 42.2574° : -71.83458°, hardwood, 11 Apr. 2013, Miettinen 16044 & Käppi (H 7005770, designated here, MBT386590).

Irpex cinnamomeus Fr., *Epicrisis*: 524. 1838 (fide Ryvarden 1982a).

Thelephora episphaeria Fr., *Elenchus Fung.* **1**: 225. 1828.

Lectotype: USA, North Carolina, Burke Co., Salem, Schweinitz (UPS F-173519, designated here, MBT386591). **Epitype:** USA, New York, Essex Co., Huntington Wildlife Forest, Adjidaumo flow, 42.2574° : -71.83458°, *Fagus grandifolia*, 18 Sep. 2013, Miettinen 16956.2 (H 7008916, designated here, MBT386592).

Hymenochaete agglutinans Ellis, *Bull. Torrey Bot. Club* **5**: 46. 1874. **Lectotype:** USA, New Jersey, Gloucester Co., Newfield, hardwood, 1874 Ellis (NY 00742784, designated here, MBT387111). **Epitype:** The same locality, Nov. 1881 Ellis (NY ex C. Roumeguère, Fungi selecti exsiccati #4540, designated here, MBT386593).

Sistotrema fuscescens and *H. olivaceum* were described in the same paper. This very common North American fungus is conspicuous and easy to identify among *Hydnoporia* with its irpicoid hymenophore. Material we have seen is uniform, and the following discussion focuses on nomenclature. However, it should be said that ITS sequences show some variation, more than is typical for most other *Hydnoporia* spp. (Fig. 2). Our own sampling is limited, so we refrain making any conclusions based on this.

Banker (1914) chose to synonymize *S. fuscescens* with *S. olivaceum*, and as he has been widely followed by later authors, the latter name should be used for this species. Ryvarden (1982a) designated a lectotype for *S. olivaceum* (Schweinitz 540, PH). Parmasto *et al.* (2014) studied the lectotype as well as an isoelectotype in UPS (Parmasto 2001). There are two specimens, possibly parts of the same collection, with the same Schweinitz number (540), but filed under different herbarium numbers. This makes it necessary to amend Ryvarden's lectotypification. **Lectotype** for *Sistotrema olivaceum* Schwein., designated here: USA, Pennsylvania, Salem, PH00062632 (MBT386594).

Since *S. fuscescens* is the type species of *Hydnoporia*, we need to secure the identity of the species through typification. Banker (1914) stated a type probably does not exist, and mentioned only one specimen from the Schweinitz collection, '580–7 Syn. Fung. I. cinnamomeus Epic. 19. *Irpex fuscescens* Schw. Beth.', which represents typical *H. olivacea*. That specimen is not available as a lectotype, because it was evidently collected in Bethlehem, Pennsylvania, where Schweinitz moved in 1821 (Rogers 1977), and not in North Carolina, the type locality (Schweinitz 1822). Schweinitz's herbarium in PH is fully available online under plants.jstor.org, and it does not contain any other specimens under the name *S. fuscescens*. However, an authentic specimen of *S. fuscescens* from *locus classicus* exists in Fries's herbarium in Uppsala, and therefore we designate it as the lectotype here. After considering the intraspecific ITS variation and the fact that the type specimen is sterile, we also designate a modern, sequenced epitype.

Thelephora episphaeria was described by Fries (1828) based on a Schweinitz collection from North Carolina. Parmasto (2001) selected another Schweinitz's collection from Pennsylvania to serve as a type (Bethlehem, on *Diatrype*, Schweinitz 723, PH 00077588). In our opinion, this choice cannot be supported because Fries must be considered the single author of this species and material seen by him should be selected for typification. Since only one specimen exists in Fries's herbarium, collected by Schweinitz, it should be designated as the lectotype of *T. episphaeria* (indicated above). In older literature, *T. episphaeria* was considered very close or probably identical to *H. corrugata*, although with some reservations (Bondartseva & Parmasto 1986, Parmasto 2001). After studying the lectotype of *H. episphaeria*, we cannot agree with this opinion - both setal and spore measurements certainly point towards *H. olivacea*. The latter species is able to produce rather thin and completely smooth basidiocarps. In this condition, it can be mistaken for other *Hydnoporia* species. Here we designate a recent, sequenced specimen of *H. olivacea* with a smooth hymenium as an epitype for *T. episphaeria*.

Another synonym of *H. olivacea* introduced here is *Hymenochaete agglutinans*. This species was described from New Jersey (Ellis 1874) and it represents sterile films on branches of angiosperm trees and shrubs (Graves 1914, Burt 1918, Parmasto 2001). Reeves & Welden (1967) placed *H.*

agglutinans in the synonyms of *H. corrugata* although their opinion on connection of sterile mats with the latter species was merely a matter of belief. We studied the original specimen of *H. agglutinans* from NY (designated above as the lectotype) and cannot agree with Reeves & Welden, because the NY specimen belongs to a truly dimitic species with wide setae. Moreover, there is another specimen of *H. agglutinans* collected by Ellis in or near the type locality in 1881 (distributed in C. Roumeguère's *Fungi selecti exsiccati*, #4540), which represents a basidiocarp developed on the surface of a sterile patch. Morphologically, the sterile stage of this collection is identical to the *H. agglutinans* lectotype, composed of very thick-walled, almost unbranched and dark-coloured skeletal hyphae and sharp-pointed setal hyphae, while the basidiocarp is undoubtedly a young specimen of *H. olivacea* with irregularly poroid to irpicoid hymenophore. Therefore, we consider *H. agglutinans* a synonym of *H. olivacea*. Burt (1918) stated that the type material of *H. ambiens*, also described from New Jersey, represents the same sterile stage as *H. agglutinans*.

Hydnoporia rhododendri (Corfixen & Parmasto) Spirin & Miettinen, **comb. nov.** MycoBank MB830596. Figs 5, 6.
Basionym: *Hymenochaete rhododendri* Corfixen & Parmasto, *Karstenia* **57**: 65. 2017.

Basidiocarps annual or perennial, effused-reflexed, leathery, first cupulate or umbonate, 0.5–1 cm in diam, 0.2–0.4 mm thick, later fusing together and up to 10 cm in longest dimension; reflexed part 1.5–4 mm wide. Pileal surface uneven, finely tomentose, matt, first indistinctly zonate and ferruginous brown, later darkening to blackish brown. Pileal margin sharp, more or less even, a bit incurved in dried specimens, margin of resupinate parts sharply delimited and partly detaching from the substrate, first pale cream coloured to yellowish, then concolorous with hymenium. Hymenial surface even or indistinctly tuberculate, pale brown, in older basidiocarps often rimose, with greyish hues. **Section:** Tomentum loose, brown, 20–50 µm thick; cortex poorly visible, dark brown, 10–30 µm thick; trama duplex, upper layer loose, straw-yellow to pale ochraceous, 60–80 µm thick, lower layer dense, dark brown, 40–80 µm thick; hymenium / subhymenium pale cream to pale ochraceous, 40–60 µm thick, with dark coloured embedded or projecting setae. **Hyphal system** dimitic; hyphae with simple septa. Setal hyphae originating deeply in upper tramal layer, sharp-pointed, very thick-walled, lateral or pleural, some distinctly bent, a few vertically arranged and penetrating hymenial layer, dark ferruginous brown, 90–240(–350) × 5.2–9.4 µm (*n* = 11/2). Skeletal hyphae rather poorly differentiated, located in the uppermost parts of basidiocarps, dark-brown, mostly unbranched and not septate, 2–3.5 µm in diam. Generative hyphae mostly with thickened walls, yellowish to brownish, 2.3–4.0 µm in diam (*n* = 40/1), vertically and tightly arranged in tomentum, more or less horizontal and parallel in cortex and upper tramal layer, irregularly interwoven to subparallel in lower tramal layer; subhymenium distinct, 20–40 µm thick, hyphae hyaline, with thin or slightly thickened walls, vertically and tightly arranged, 2.1–3.1 µm in diam (*n* = 10/1). **Tramal / hymenial setae** mostly sharp-pointed, normally with widened basal part, dark ferruginous brown, 53–99 × 6.2–18.7 µm, *L* = 71 µm, *W* = 10.5 µm, *Q* = 7.19, rarely pleural or bifurcate, some with scarce encrustation, embedded or projecting up to 15–40 µm above hymenial cells, usually covered by semi-translucent sheaths of hyphidia. **Basidia** narrowly clavate,

4-spored, 11.9–19.8(–22.0) × 2.4–3.2(–3.6) µm (*n* = 40/3). **Basidiospores** allantoid, slightly to distinctly curved, (3.8–)3.9–5.2(–5.6) × (1.1–)1.2–1.6(–1.7) µm, *L* = 4.56 µm, *W* = 1.33 µm, *Q* = 3.44.

Distribution and ecology: Grows on branches of *Ericaceae*. Widely distributed although uncommon in mountains of temperate Eurasia.

Notes: *Hydnoporia rhododendri* is phylogenetically a sister species of *H. tabacina*, but should be easily identifiable by its narrow and rather short spores and its host. The Central American *H. lenta* has similar spores but it differs in having distinctly shorter (45–65 × 8.5–16 µm), blunt setae with wide lumen (Léger 1990). The only European specimen (TAAM 189353) sequenced for this study shows 9 bp difference in ITS region from two East Asian collections, and no *tef1* sequence is available for it. Because of negligible morphological differences between European and Asian specimens, we currently consider them to belong to the same species.

Hydnoporia rimosa (Lloyd) Spirin & Miettinen, **comb. nov.** MycoBank MB830597. Figs 5, 6.
Basionym: *Hymenochaete rimosa* Lloyd, *Bot. Mag. Tokyo* **44**: 92. 1930.

Typus: Japan, Tōhoku, Sendai, 24 Oct. 1920, Yasuda (TNS F-203210, **lectotype** designated here, MBT387146, studied).

Basidiocarps perennial, effused, leathery, 0.1–0.2(–0.3) mm thick, covering several cm. Margin sharply delimited and firmly attached to the substrate, first whitish, later ferruginous brown (in mature basidiocarps normally darker than hymenial surface). Hymenial surface even or indistinctly tuberculate, first grey to greyish ochraceous, later pale chocolate brown, in mature basidiocarps strongly rimose. Sterile patches and films bright ferruginous brown, up to 7 cm in longest dimension, rather firm, associated with basidiocarps or growing solitary. **Section:** Subiculum poorly visible, first pale coloured, in perennial basidiocarps dark brown to almost black, about 20 µm thick; trama cream coloured to pale ochraceous, 30–50 µm thick; hymenium / subhymenium grey to pale brown, 30–40 µm thick, with dark coloured, mostly embedded setae. Perennial basidiocarps stratified (2–3 layers divided by dark lines). **Hyphal system** monomitic; hyphae with simple septa. Setal hyphae present in sterile films, blunt-pointed, very thick-walled, lateral or pleural, brown, 75–205 × 6–9.5 µm. Skeletal-like hyphae often abundant in subiculum and lowermost parts of trama, brownish to dark-brown, occasionally branched and septate, 2–4.5 µm in diam. Generative hyphae mostly with thickened walls, in sterile films yellowish to brownish, 3–5.5 µm in diam, irregularly arranged to subparallel; in subicular layer and upper trama pale to dark brown, clearly thick-walled, more or less horizontal and parallel to the substrate, in lower trama and subhymenium hyaline to pale brown, mostly vertically arranged (2.1–)2.3–3.6(–4.0) µm in diam (*n* = 20/2). **Tramal/hymenial setae** rather blunt-pointed, normally with distinctly widened basal part, dark ferruginous brown, 50–144 × 6.6–18.2 µm (*n* = 100/5), *L* = 75 µm, *W* = 10.3 µm, *Q* = 7.41, often pleural and with apical crystalline cape, embedded or projecting up to 15–60 µm above hymenial cells, associated with simple hyaline hyphidia 1.5–3.5 µm in diam. **Basidia** narrowly clavate, 4-spored, (11.1–)11.3–18.5(–20.3) × (3.2–)3.5–4.3 µm (*n* = 20/3). **Basidiospores** cylindrical, straight to

slightly curved, (4.1–)4.2–6.3(–6.9) × (1.8–)1.9–2.3(–2.5) µm, L = 5.22 µm, W = 1.99 µm, Q = 2.64.

Distribution and ecology: Occurs on both living and on recently dead branches of angiosperms in East Asia.

Notes: *Hydnoporia rimosa* is an East Asian relative of *H. corrugata* and *H. diffissa*. It seems to be a pathogen, starting to develop abundant sterile mycelium while the host species is still alive and continuing to grow after the host dies. We have no Japanese sequenced material, but morphologically the type fits well with sequenced specimens from Russian Far East. However, our application of the name *H. rimosa* should be revised against material from Honshu. Sequence data shows that there is a fourth species in this complex in China and Korea (Fig. 2).

Hydnoporia rimosa was described in Ito (1930a, as *Hymenochaete r.*). Ito directly cited Lloyd's description of the species and the correct species author is Lloyd. Ito also provided a list of specimens, adding to Lloyd's description. Both components are part of the protologue (see ICN Art. 6.13 footnote), and therefore the specimens Ito listed are to be considered syntypes, which have priority over other original material when selecting the lectotype (Art. 9.12). This is relevant because Stevenson & Cash (1936) chose a lectotype for *H. rimosa*, from Lloyd's herbarium. That specimen may have been part of the original material, but not a syntype since it was not cited in the protologue. Thus our lectotypification supersedes that of Stevenson & Cash (Art. 9.19).

Hydnoporia subrigidula (S.H. He & Hai J. Li) Miettinen & K.H. Larss., **comb. nov.** MycoBank MB830598.

Basionym: *Pseudochaete subrigidula* S.H. He & Hai J. Li, *Mycol. Prog.* **12**: 335. 2013.

Notes: The species was introduced as a close relative of *Hymenochaete rigidula* from China (He & Li 2013). However, identity of the latter species is still unclear (see discussion under Excluded species). Nevertheless, the morphological description as well as available DNA sequences confirm that *P. subrigidula* is a member of *Hydnoporia*.

Hydnoporia tabacina (Sowerby) Spirin, Miettinen & K.H. Larss., **comb. nov.** MycoBank MB830599.

Basionym: *Auricularia tabacina* Sowerby, *Coloured Fig. English Fungi* **1**: 14. 1797.—*Thelephora tabacina* (Sowerby) Fr., *Systema Mycologicum* **1**: 437. 1821.

Typus: Sweden, Skåne, Fries (UPS F-175737, **lectotype** designated here, MBT386595, studied).

Synonym: *Stereum intricatum* Lloyd, *Mycol. Writings* **7**(67): 1157. 1922. **Typus:** Japan, Hokkaido, Tomakomai, Iburi, *Alnus*, 20 Dec. 1904, Niidjima 706 [TNS F-200336, **lectotype** by Ito (1930b), studied].

Notes: We consider *H. tabacina* a Holarctic species in this paper. There is, however, some minor variation in ITS (Fig. 2) and clearly two separate *tef1* groups (Fig. 2). European specimens from Nizhny Novgorod, Russia, England and Finland show a divergent *tef1* sequence of 11 bp (1.3 %) from the rest of the material, though the easternmost European specimen from Perm (*Kotiranta* 25205) falls within the Asian-North American clade.

The five European ITS sequences (excluding the Perm specimen) show a 1 bp difference against the rest as well, in line with the *tef1* division. We see no differences between these genotypes in morphology or host species range. The species inhabits branches and more rarely logs of many angiosperm trees and shrubs but sometimes occurs also on conifers (especially on *Picea*).

Clearly, the *H. tabacina* complex deserves to be studied further to determine if more than one species is involved. Answering this question is beyond the scope of this paper, and will require more extensive sampling particularly from North America and Europe, with sequences of several fast-evolving markers. If the *tef1* genotypes would turn out to represent different species, then the European genotype should be called *H. tabacina*. There would be several American and Asian old names to choose from for the Asian-North American species as discussed below.

Hydnoporia tabacina was described many times. Its oldest names include *Helvella nicotiana* Bolton 1792 (England, *Syringa*), *Auricularia tabacina* Sowerby 1797 (England, angiosperms), *Thelephora avellana* Fr. 1821 (Sweden, *Corylus*), *T. cerasi* Pers. 1822 (France, *Cerasus*), *T. juratensis* Pers. 1822 (France, *Fagus*), *T. crocata* Fr. 1828 (South Europe, angiosperms), and *T. imbricatula* Schwein. 1832 (USA). Fries (1821: 437) sanctioned Sowerby's *A. tabacina*, and we select here a lectotype from Sweden in accordance with ICN Art. 9.3 for fixing its concept.

The choice of lectotype requires justification. Fries treated the species in the sanctioning work *Systema Mycologicum* (Fries 1821: 437), where he mentions that he has seen fresh material ("v. v.") and that the main host is *Corylus*. The specimen we selected as a lectotype was collected from Skåne by Fries and labelled *Stereum tabacinum*. Its host is beyond doubt *Corylus avellana*. As usual, no collecting date is provided. He himself mentions material of *H. tabacina* from Skåne (under the name *Stereum ferrugineum*) in *Observationes* 2 (Fries 1818: 274). Strid (1995: 44) points out that *Observationes* were "largely based on material that he gathered between 1813 and 1815". Later Fries (1857) wrote that he received several collections from Skåne in 1819, which prompted him to describe several species in *Systema Mycologicum*. Whichever the case, all indications are that the specimen from *Corylus* from Skåne was collected before the sanctioning and was used as a source of the sanctioning description.

Hymenochaete konradii from the Czech Republic was described as having "dendrophyses" in hymenium (Léger 1985), and it is the only difference from *H. tabacina*. We observed those branched hymenial cells in several typical specimens of the latter species, and this character is certainly not sufficient for species delimitation in this group. Thus, *H. konradii* might be a synonym of *H. tabacina*, but this needs to be confirmed. Bresadola (1920) added *Daedalea lirellosa* Pers. to the synonyms of *H. tabacina*, but his conclusion seems to be wrong; we will discuss this question in a forthcoming paper.

Hymenochaete intricata was described from Japan (Ito 1930b). This species was considered as widely distributed on angiosperm substrates in Northeast China and Russian Far East, while *H. tabacina* was supposedly absent from this area (Bondartseva & Parmasto 1986, Dai 2010). There are small differences in spore and setal sizes between East Asian and other Eurasian material of *H. tabacina* (Tables 1, 2). However, our DNA data (ITS and *tef1*) do not support separation of East Asian specimens, i.e. *H. intricata*, from other Asian and North American specimens of *H. tabacina*.

Hydnoporia tabacinoides (Yasuda) Miettinen & K.H. Larss., **comb. nov.** MycoBank MB830601.

Basionym: *Irpex tabacinoides* Yasuda, *Bot. Mag. Tokyo* **33**: 189. 1919.

Notes: Results by He & Dai (2012) indicate that this species belongs to *Hydnoporia*. Ryvarden (1982a) provided a modern description of the species based on Japanese material (as *Hydnochaete tabacinoides*). He considered it similar to *Hydnoporia olivacea*. The description by Dai & Niemelä (2006) does not fully agree with Ryvarden's, for instance the spore size is different. While it appears that sequences published as *H. tabacinoides* from China represent a separate species, they should be checked against authentic material to ascertain their identity. In any case, all morphological descriptions indicate that *H. tabacinoides* is a member of *Hydnoporia*.

Hydnoporia yasudai (Imazeki) Spirin & Miettinen, **comb. nov.** MycoBank MB830602.

Basionym: *Hymenochaete yasudai* Imazeki, *Bull. Tokyo Sci. Mus.* **2**: 6. 1940.

Typus: **Japan**, Tokyo, Minami-Tama Gun, Sainokami Goryochi, *Abies firma* (dry branches), 10 Oct. 1939, Imazeki (**holotype** TNS F-207357, studied).

Notes: *Hydnoporia yasudai* is an East Asian species inhabiting dry branches and bark of *Pinus* spp., rarely other coniferous trees. It was described from Japan (Imazeki 1940), and found also in China (Dai 2010) and Russian Far East (Bondartseva & Parmasto 1986). Basidiocarps of *H. yasudai* are usually sterile; however, the species is easily identifiable due to peculiar moniliform, thick-walled hyphidia and its host preferences. Basidiospores of *H. yasudai* are similar to other *Hydnoporia* species, cylindrical and rather small, $4.4\text{--}6.1 \times 2\text{--}2.3 \mu\text{m}$, not ellipsoid and large as described in some recent manuals (Bondartseva & Parmasto 1986, Dai 2010).

ITS data indicates that *H. yasudai* is a complex containing three to six species (Fig. 2). Our collections from Russia derive from *Pinus pumila* and the type from *Abies firma* in Japan. The type is in bad condition and contains very few spores. It is otherwise similar to the Russian specimens we have sequenced except that the Russian specimens are bright-coloured whereas the type is quite dull, dark brown. For now, the Russian specimens are best called *H. yasudai*, but clearly Japanese, sequenced material is needed to settle nomenclature in the complex.

Excluded species

Hymenochaete allantospora Parmasto, *Folia Crypt. Estonica* **37**: 58. 2000.

Notes: Allantoid basidiospores of this species are the only morphological feature, which might imply *Hydnoporia*. They are, however, much longer than in any *Hydnoporia* spp. treated above, *ca.* $8\text{--}12 \times 2.2\text{--}2.9 \mu\text{m}$. Large, suburniform basidia ($17\text{--}27 \times 4\text{--}5 \mu\text{m}$), well-differentiated skeletal hyphae and regularly shaped and rather rare setae indicate that *H. allantospora* is a member of *Hymenochaete* s. str.

Hymenochaete rigidula Berk. & M.A. Curtis, *J. Linn. Soc., Bot.* **10**: 334. 1869.

Notes: This species was described from Cuba (Berkeley & Curtis 1869), and no sequenced material is available from the Caribbean. Based on the description by Parmasto (2001) we are on the opinion that *H. rigidula* s. str. probably belongs to *Hymenochaete*. He & Dai (2012) reported a Chinese species under this name. Their "*H. rigidula*", also present in Korea, is a separate species from other *Hydnoporia* (Fig. 2). They did not study the type, and we think it is unlikely that their *H. rigidula* belongs to the species described from the Caribbean

Hymenochaete sallei Berk. & M.A. Curtis, *J. Linn. Soc., Bot.* **10**: 333. 1869.

Notes: A Chinese sequence (FJ481043) is deposited in the INSDC database under the name *H. sallei*. This sequence from Jiangsu or Anhui represents, if it can be trusted, a third species in the *Hydnoporia tabacinoides* complex (Fig. 2). *Hymenochaete sallei* is, however, a typical member of *Hymenochaete* (Parmasto *et al.* 2014) and considered a synonym of *H. rheicolor* by Parmasto (2001). The name has apparently been misapplied to the sequence in question.

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